

A REASSESSMENT OF THE RELATIONSHIPS OF  
PERMIAN DICYNODONTIA (REPTILIA, THERAPSIDA) AND A  
NEW CLASSIFICATION OF DICYNODONTS

By

MICHAEL A. CLUVER

*South African Museum, Cape Town*

&

GILLIAN M. KING

*Department of Zoology and University Museum, Oxford*

(With 40 figures)

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ABSTRACT

The type specimens of several genera of Permian dicynodonts have been re-examined and, where possible, prepared. Diagnoses of the following genera have been drawn up: *Eodicynodon*, *Endothiodon*, *Pristerodon*, *Tropidostoma*, *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*, *Pelanomodon*, *Dicynodon*, *Robertia*, *Diictodon*, *Emydops*, and *Kingoria*. Other genera have also been discussed.

Suites of derived characters have been formulated for each genus and used to draw up a cladogram of the phylogenetic relationships of the genera. A classification has been erected from the cladogram, using a methodology based on cladistic principles.

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## INTRODUCTION

The Dicynodontia were a large group of herbivorous therapsids that probably arose during the Permian. By the end of the Permian they were the dominant herbivorous element of the fauna, but subsequently diminished in numbers with only a few representatives surviving into the Triassic. There is evidence that some forms were distributed world-wide.

The earliest forms generally recognized as belonging with the Dicynodontia (*sensu* Romer 1966) are from the *Tapinocephalus* Zone of the Beaufort Group of South Africa. These were small animals (skull length up to approximately 10 cm) that retained postcanine teeth but lacked incisors. By contrast the latest Triassic forms were large animals (skull length approximately 570 cm) that had lost all trace of teeth and had developed to the full the horny beak characteristic of the group.

In their skull characteristics dicynodonts constitute one of the most specialized of the therapsid groups. The preorbital region is short and in later forms the premaxilla and maxilla are edentulous, apart from the variably present pair of large canine tusks. In these forms a horny beak, similar to that of chelonians, is generally considered to have been present. The zygomatic arch flares laterally and is emarginated ventrally so that it becomes a narrow bar running posteriorly and dorsally in the skull. Posterior to the zygoma the squamosal flares laterally and is overlain anteriorly by the quadrate and quadratojugal. The lateral plate of the squamosal and the external surface of the zygoma provide attachment areas for jaw adductor musculature (the adductor externus lateralis), a situation unknown in therapsids outside the cynodonts. The quadrate forms a double condyle. The articular surface of the lower jaw is shallowly concave, then convex more posteriorly, and permits a sliding action on the quadrate. It is generally agreed (Watson 1948; Crompton & Hotton 1967; Cluver 1971) that such sliding would allow areas of the palate and the lower jaw to come into contact and triturate food matter. Protraction of the lower jaw would also allow the anterior tips of the upper and lower jaws to make contact and effect a 'beak-bite'.

In the palate the lateral pterygoid process is much reduced from the pelycosaur condition and directed anteriorly. A secondary palate formed by the posterior extension of the premaxilla and the medial extension of the palatines is present in later forms and is incipient in early representatives. Palatal teeth are lost.

The lower jaw does not have a coronoid bone. A mandibular fenestra between dentary and angular is present, and adductor muscles inserted on the outer surface of the jaw ramus as well as internally.

This character suite is used to define the Dicynodontia in the present paper. Any forms that fall within this definition will be referred to informally as dicynodonts, rather than dicynodontoids, dicynodontids, and so on.

Although there is a growing body of knowledge concerning the morphology and functional anatomy of dicynodonts, it has proved difficult to synthesize individual contributions since the taxonomy of the complete group has not been adequately worked out, despite the efforts of several workers (e.g. Toerien 1953; Cox 1959; Keyser 1975; Keyser & Cruickshank 1979; Cluver & Hotton 1981). Hammer & Cosgriff (1981) noted recently that 'the unresolved issues [touched upon here] are typical of the currently fluid state of dicynodont taxonomy and emphasize how little is understood about the natural groupings within this infraorder'.

There are various reasons for this state of affairs: the abundance of dicynodont material, the numerous taxa created on inadequately prepared and figured material, the loss of key type specimens, and the intractability of the matrix in which the earliest forms have been found. The present authors believe that any attempt at classification of dicynodonts should be based as far as possible on the re-examination of original type material, and that only type material that is reasonably well preserved and prepared should be considered. Forms that cannot be adequately diagnosed (especially incomplete or single specimens) should be left for the present *incertae sedis* until further preparation or additional specimens make their relationships clearer.

To this end type and other material in South Africa, the United States, and Great Britain was re-examined by either or both of the authors. Where possible, further preparation of the specimens was carried out. Since most of the described species and genera are of Upper Permian age and the taxonomy is most confused among these, it was decided to pay particular attention to the establishment of adequate diagnoses of these forms. The Triassic forms, in any case, have recently been reviewed by Keyser & Cruickshank (1979).

Furthermore, it was felt that diagnoses should as far as possible take into account derived characters, as opposed to shared primitive characters, so that relationships among genera could be established according to methods of Hennigian systematics.

The review has been confined to the generic level. The status of species within genera has not been discussed but it is recognized that this must be attempted at some future stage.

The genera reviewed and classified in this paper are: *Eodicynodon*, *Endothiodon*, *Pristerodon*, *Tropidostoma*, *Rhachiocephalus*, *Oudenodon*, *Aulacephalodon*, *Pelanomodon*, *Dicynodon*, *Robertia*, *Diictodon*, *Emydops*, *Myosaurus*, *Cistecephalus*, and *Kingoria*. All these genera, with the exception of *Eodicynodon* and *Myosaurus*, are from the Upper Permian of the Beaufort

Group of the South African Karoo Supergroup. *Eodicynodon* is from the upper Waterford Formation of the preceding Ecca Group (Rubidge & Oelofsen 1981), while *Myosaurus* is from the base of the Triassic of the Beaufort Group.

Assignment of localities to the various stratigraphic zones of the Beaufort Group follows the work of Kitching (1977), which in the opinion of the authors presents the most practical guide to Karoo biostratigraphy.

## REDESCRIPTION AND DIAGNOSIS OF PERMIAN GENERA

Genus *Eodicynodon* Barry, 1974

Type species *Eodicynodon oosthuizeni* Barry, 1974

### *Type material*

Skull lacking anterior part of snout and lower jaw, ROZ 1.

### *Locality*

Zwartskraal, Prince Albert district, Cape Province.

### *Stratigraphic horizon*

Upper Waterford Formation, Ecca Group (Rubidge & Oelofsen 1981).

### *Remarks on the type specimen*

In a series of papers Barry (1972, 1974, 1975) described the stratigraphic occurrence, morphology, and systematic position of *Eodicynodon oosthuizeni*. Barry's 1974 paper contains a full description of the specimen. The most important features of the skull that set it apart from other dicynodonts are the paired vomers and premaxillae and the strong lateral processes of the pterygoids (Figs 1-2). These features represent the primitive therapsid condition as seen in pelycosaurs.

### *Description of additional specimens of Eodicynodon*

Barry (1974) listed other specimens from the same locality as the holotype ROZ 1, and two of these specimens (ROZ 9 and 11) have since been prepared out of extremely hard matrix with the aid of dilute acetic acid to expose all bone completely. Details of these specimens complement what has already been described of *Eodicynodon* and, in view of the position of *Eodicynodon* as unquestionably the most primitive South African dicynodont known, it is felt warranted to describe the additional specimens in some detail. ROZ 9 is an incomplete skull with lower jaw and associated left forelimb and manus (Figs 3-6); ROZ 11 is an incomplete skull lacking lower jaw (Figs 7-8). The estimated original lengths of the two skulls are 80 mm (ROZ 9) and 70 mm (ROZ 11). The following description is based on both specimens.

A striking feature of the maxilla is a deep notch in the palatal rim in front of the well-developed tusk (Figs 5-6), so that in lateral view the rim is deeply

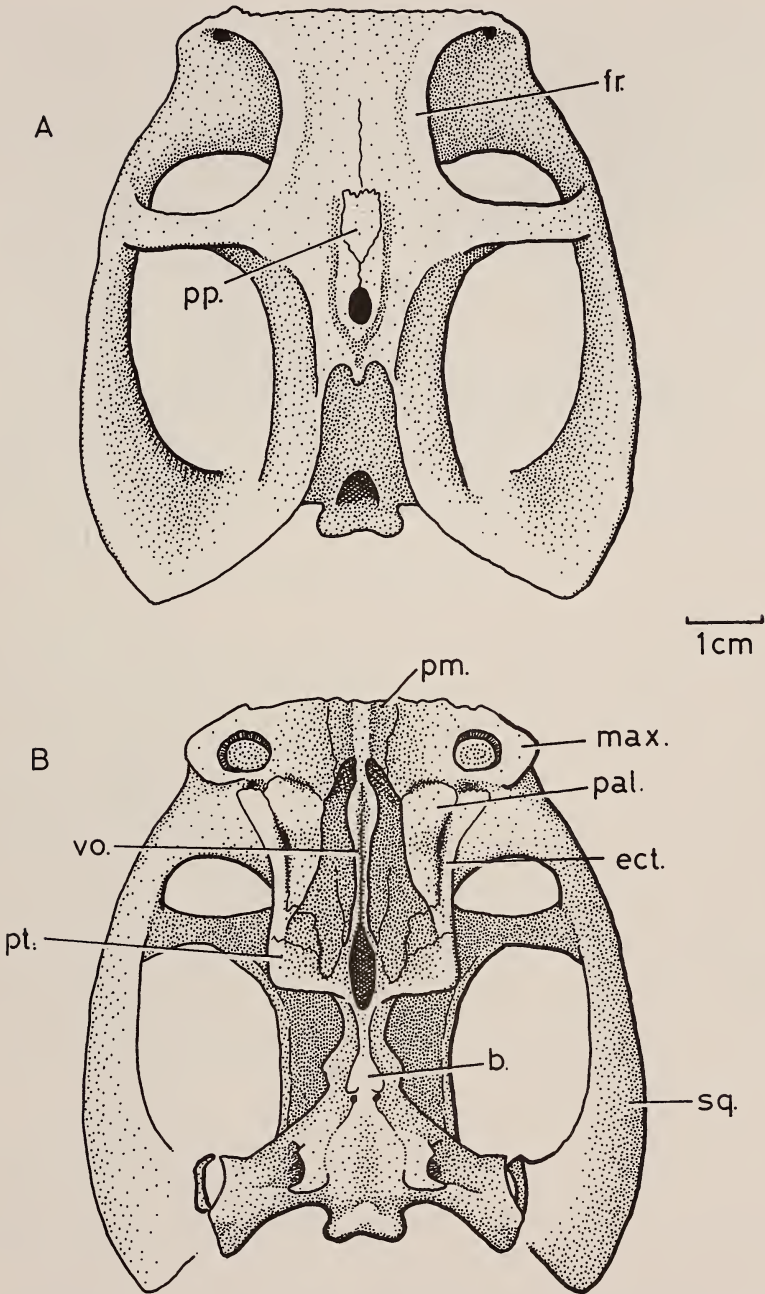


Fig. 1. *Eodicynodon oosthuizeni*. Type specimen ROZ 1, from Zwartskraal, Prince Albert. A. Dorsal view. B. Ventral view.

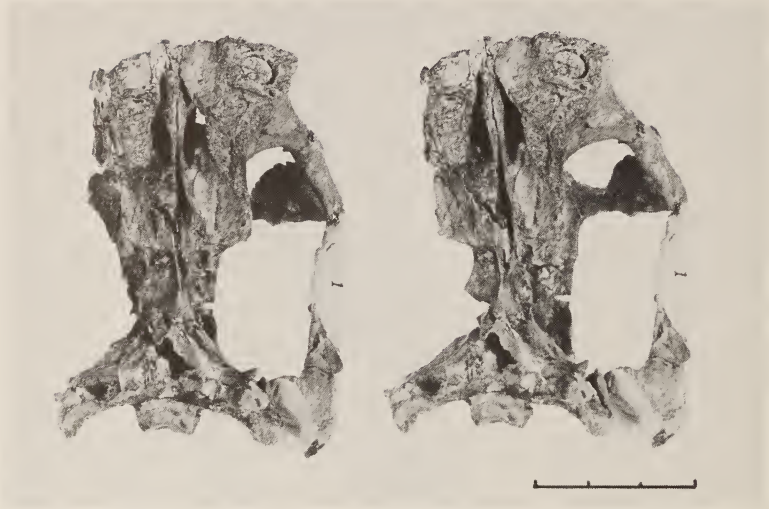


Fig. 2. *Eodicynodon oosthuizeni*. Type specimen ROZ 1. Stereophotograph of skull in ventral view. Scale in cm.

incised in a way not seen in other dicynodonts. In ROZ 9 an empty socket medial to the base of the right tusk, as well as what appears to be the base of a small, broken-off tooth in the corresponding position on the left side, indicate that teeth other than the tusks were present. In ROZ 11 there are two small teeth on the alveolar margin in line with the centre of the tusk. Two teeth are also present medial to the tusk. On the right side one small and one larger tooth are present, but on the left side only a single tooth can be made out. Small teeth are also present on the lower jaw of ROZ 9 (see below).

In the midline, where the premaxilla meets the vomerine interchoanal septum, a small portion of the premaxillary crest is preserved.

In the upper part of the incompletely preserved snout of ROZ 9 the floor of a fairly extensive maxillary antrum lies behind the root of the tusk. A narrow, slit-like opening leads through the anteroventral border of the orbit into the antrum on the left side; no counterpart of this opening can be seen on the right side of the skull.

The choanal opening in the palate differs from that of other dicynodonts in that a narrow, slit-like portion extends far forward to the level of the centre of the base of the tusk. Posteriorly the choana becomes shallow and wide between the pterygoids. The ventral edge of the vomerine septum is excavated as a deep trough widening posteriorly to merge with the interpterygoidal vacuity. In the roof of the trough a longitudinal suture indicates the meeting of the paired vomers.

The palatine has a swollen anteroventral palatal portion that does not project far medially into the choana. The ventral surface of this portion is rugose, contrasting sharply with the smoothly finished surrounding palatal

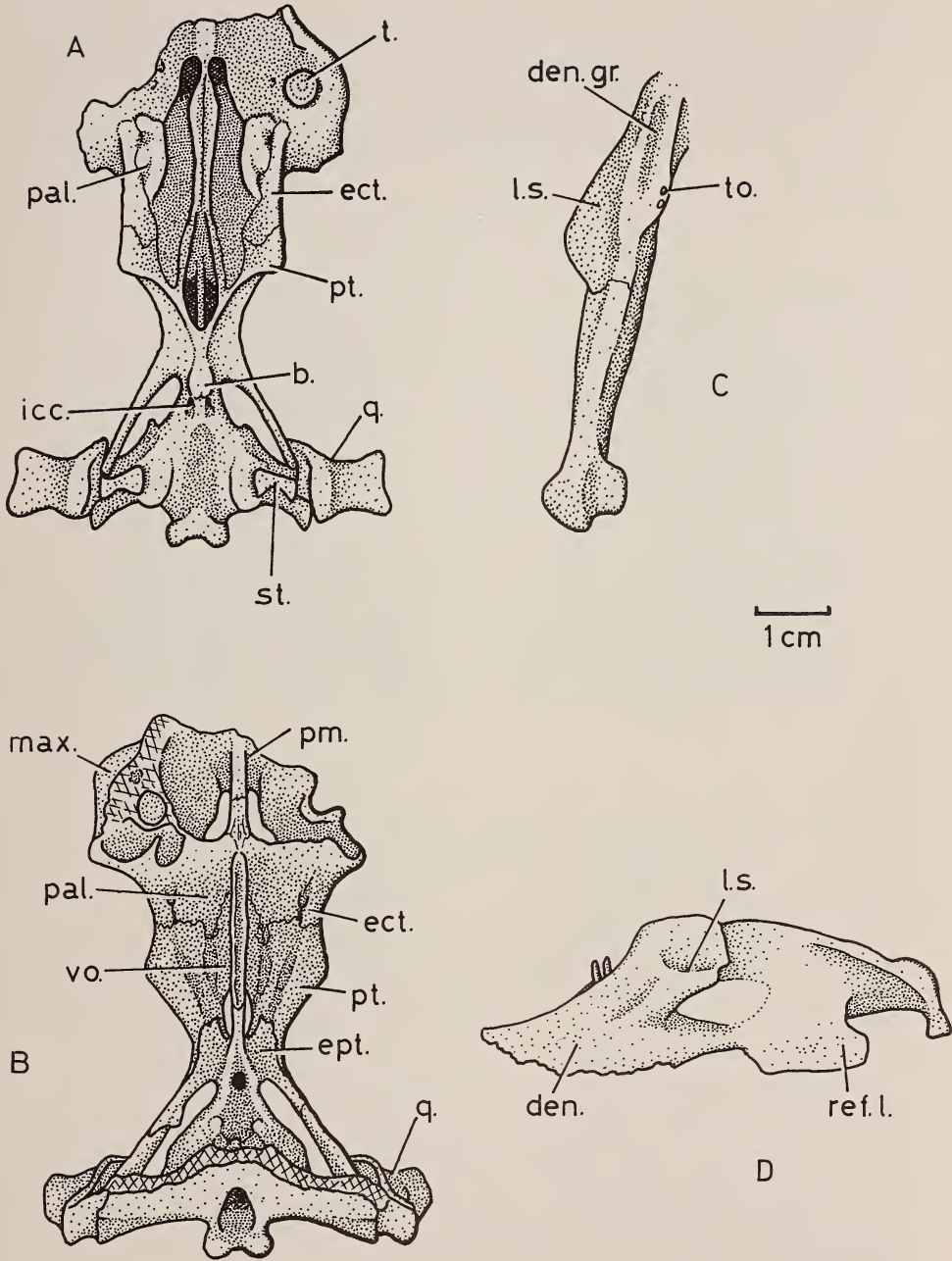


Fig. 3. *Eodicynodon oosthuizeni*. ROZ 9, from Zwartzkraal, Prince Albert. A-B. Skull in ventral and dorsal views. C-D. Left ramus of lower jaw in dorsal and lateral views.

bones, and evidently carried a horny pad during life. Dorsally the palatine curves upward towards the midline to form a roof for the choanal passage, and posteriorly it terminates as a narrow wedge alongside the interpterygoidal vacuity. A lateral palatal foramen between the palatine and ectopterygoid opens dorsally on to the posterior surface of the jugal, continuing upward as a short groove.

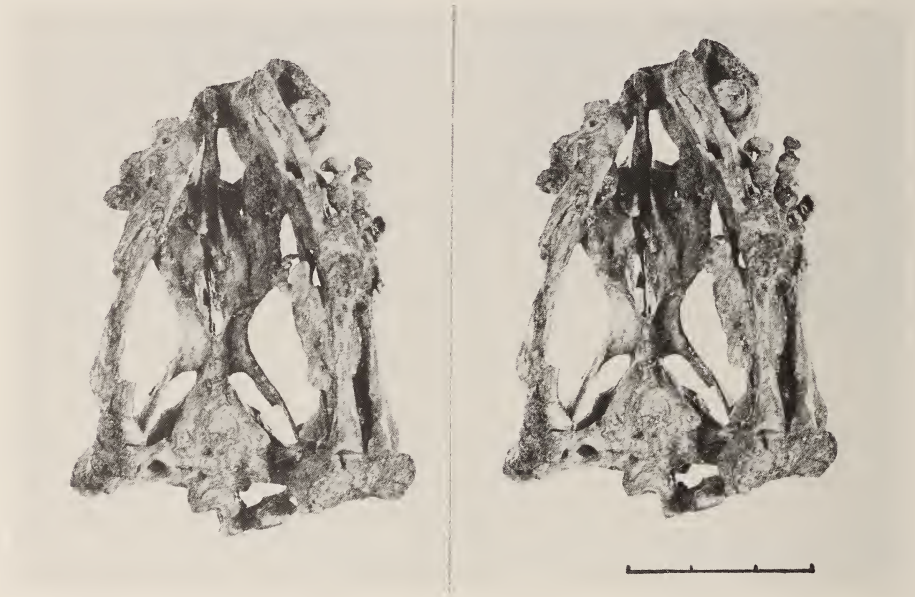


Fig. 4. *Eodicynodon oosthuizeni*. ROZ 9. Stereophotograph of skull and lower jaw in ventral view, with partial left forelimb. Note deep notch in palatal rim anterior to left maxillary tusk. Scale in cm.

Dominating the ventral view of the skull is a prominent ventrally directed pterygoid flange or process making up the ventrolateral border of the choanal space. The posterior corner of the process is also the most ventral part of the pterygoid and compares in position with the lateral pterygoid process of non-dicynodont therapsids.

Behind the interpterygoidal vacuity the pterygoids unite and together with the basisphenoid form a prominent ventral crest in the midline. Behind the contact with the basisphenoid each pterygoid extends posterolaterally as a quadrate ramus to terminate in a recess in the medial surface of the quadrate.

The epipterygoids are represented only by their footplates, but there are indications that these bones carried anterior and posterior cartilaginous extensions during life. Thus the dorsal surface of each pterygoid carried a groove leading forward from the front of the footplate of the epipterygoid up to the pterygoid-ectopterygoid suture, and it is likely that this served to house an anterior cartilaginous extension arising from the sharply truncated anterior



edge of the footplate. The posterior edge of the footplate, also truncated, suggests the former presence of a posterior cartilaginous footplate extension, which may have reached back to a recess in the medial surface of the quadrate above the posterior tip of the quadrate ramus. Such a posterior extension of the footplate in *Lystrosaurus* has been described (Cluver 1971).

The quadrate conforms to the standard dicynodont condition and from its relationships with the articular it is clear that the anterior-posterior sliding



Fig. 5. *Eodicynodon oosthuizeni*. ROZ 9. A. Stereophotograph showing detail of palatal area of skull. B. Stereophotograph of skull and lower jaw in dorsal view. Scales in cm.

motion between the two bones, characteristic of dicynodonts, was fully developed.

The stapes, well preserved on each side, lies in the usual position between the ventrolaterally facing fenestra ovalis and the inner surface of the quadrate. The bone is remarkable in that it is pierced by a large and nearly complete stapedia foramen, broken only where two thin dorsal processes of the stapes fail to meet. Among other dicynodonts a stapedia foramen is known only in *Cistecephalus* but it is present in pelycosaur and in most other therapsid groups.

The interior of the braincase has been fully exposed and all the main features can be identified. As in other dicynodonts, the jugular foramen is large and the exoccipital is pierced by two hypoglossal nerve foramina. In the floor of the braincase the basioccipital carries a strong medial crest that rises anteriorly to terminate behind the hypophysial fossa. The sacculocochlear recess opens into the cranial cavity by means of a wide internal auditory meatus and above this the prootic carries a deep floccular fossa.

On each side of the shallow but distinct hypophysial fossa an ossified pila antotica rises some distance dorsally and anteriorly, while in front the floor of the fossa is pierced by the common internal carotid foramen. An anterior basicranial ossification, identified as the presphenoid in *Lystrosaurus* (Cluver 1971), lies clasped in the cultriform process of the parasphenoid in front of the carotid foramen. The anterior part of the cultriform process is an open, steep-sided trough, which evidently received the ventral edge of a cartilaginous interorbital septum in life.

As far as can be seen, the occipital plate conforms to the general dicynodont pattern. A portion of the squamosal is preserved on the right side of ROZ 11, overlapping the front of the occipital plate and closing off a laterally placed posttemporal fenestra. As in other dicynodonts, a channel from the anterior opening of the posttemporal fenestra leads up the lateral surface of the prootic and supraoccipital to a notch in the side of the braincase wall. This channel most probably housed a blood-vessel draining blood from the neck to the interior of the braincase before leaving the skull via the jugular vein (see Cox 1959; Cluver 1971).

Both halves of the lower jaw of ROZ 9 have been damaged and the symphyseal region is entirely lacking. The following description is based on the more complete left half (Figs 3, 6). The dentary appears to have been a relatively massive bone with a clear lateral crest for attachment of the lateral division of the jaw adductor musculature (Crompton & Hotton 1967; Cluver 1975; King 1981). Behind the symphyseal region the dorsal surface of the dentary carries a shallow groove, but posteriorly this surface is rounded and leads back to the raised dorsal boundary of the lateral dentary ledge. Behind the dorsal groove two slender teeth are situated on the inside edge of the dentary. The large mandibular fenestra is bounded by the dentary, surangular, and angular. Behind the fenestra a prominent reflected lamina of the angular extends far ventrally and is extended anteriorly and posteriorly along its ventral



Fig. 6. *Eodicynodon oosthuizeni*. ROZ 9. Stereophotograph of skull and lower jaw in lateral view, with partial forelimb and manus. Note deep notch in maxillary rim in front of tusk and distinct lateral shelf on dentary for adductor musculature.

margin. The bones of the rear of the lower jaw appear to have been displaced relative to each other and details of the space between the body of the angular and the reflected lamina cannot be made out. However, it is evident that the major part of the reflected lamina lies well below the ventral margin of the jaw and that it reaches its greatest anteroposterior extent along its ventral border. The articular is similar to that of other dicynodonts and the rounded lateral and medial condyles are clearly distinguishable from each other. A short, stout, ventrally directed retroarticular process is present.

#### *Diagnosis*

Dicynodonts with a fully developed sliding contact between convex quadrate and articular condyles and with horny beaks on upper and lower jaws.

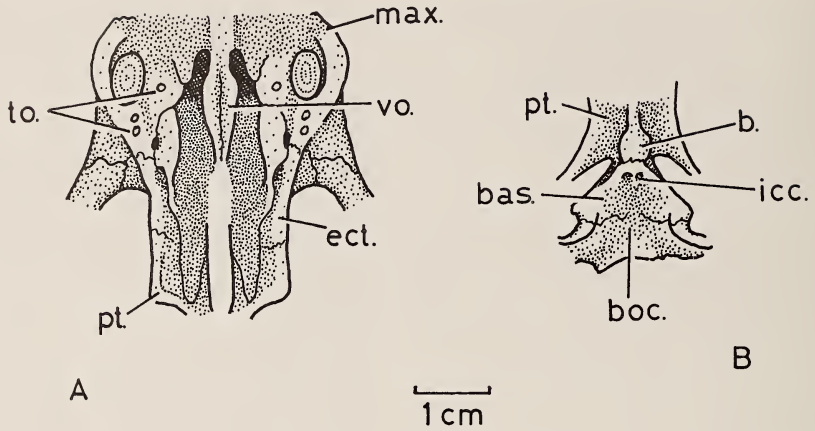


Fig. 7. *Eodicynodon oosthuizeni*. ROZ 11, from Zwartskraal, Prince Albert. A. Reconstructed palatal view of skull showing marginal position of posterior postcanine teeth. B. Basipterygoid region of skull showing bony boss on pterygoid keel.

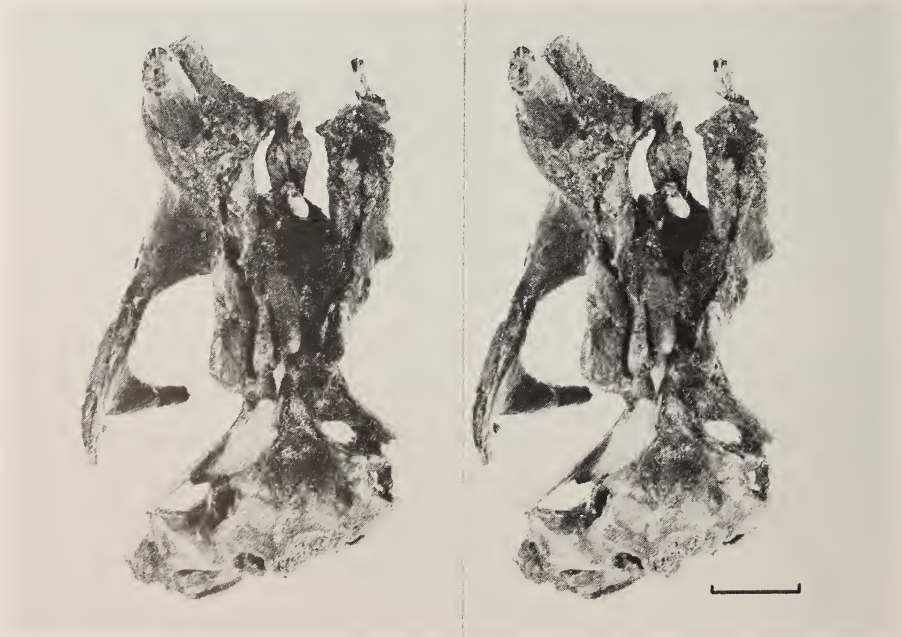


Fig. 8. *Eodicynodon oosthuizeni*. ROZ 11. Stereophotograph of skull in ventral view. Scale in cm.

Vomers paired, premaxillae paired. Strongly developed, ventrally directed lateral pterygoid process. No teeth on the anterior part of the premaxilla or on the anterior part of the dentary. Postcanine teeth present medial to the alveolar margin as well as on the alveolar margin itself. Palatal rim interrupted by deep cleft in front of maxillary tusk. Vomerine septum swollen behind the contact with the posterior premaxillary septum. Palatines bulbous and rugose. Median interpterygoidal crest enlarged to form a powerful ventral boss. Stapes pierced by stapedia foramen. Dentary with dorsally placed lateral ledge. Shallow groove in dorsal surface of the anterior part of the jaw ramus.

Genus *Endothiodon*, Owen, 1876

Type species *Endothiodon bathystoma* Owen, 1876

*Type material*

Anterior half of skull and lower jaw, BMNH R1646.

*Locality*

Sneeuwberg Range, Cape Province.

*Stratigraphic horizon*

Uncertain.

*Remarks on the type specimen*

Since Owen described the type specimen of *Endothiodon bathystoma*, various species have been added to the genus (see Haughton & Brink 1954). Cox (1964) has revised the genus and includes within it the genera *Endogomphodon*, *Esoterodon*, and *Emydochampsia*. His generic description will be used here with slight modifications based on the further examination of specimens of *Endothiodon uniseriis* (BMNH R4044, BMNH R49414) and *Endothiodon* sp. (SAM-K1233) (Fig. 9).

*Diagnosis*

Dicynodonts of medium to large size (skull length 27.5–57.0 cm). Interorbital region wide. No postfrontal bone. Intertemporal bar narrow but enlarged around the region of the pineal foramen. Median groove running posterior to the pineal foramen towards the back of the skull.

In anterior view a deep median notch in front margin of the palate. In ventral view premaxillary secondary palate deeply vaulted. Tooth row placed far posteriorly and internally. Eight to eleven long teeth on each side, distal portions bearing anterior serrations when unworn. Anterior two teeth borne on premaxilla. Horn-covered groove lateral to tooth row. Trough in ventral surface of the median vomerine plate. Large palatine meeting the maxilla

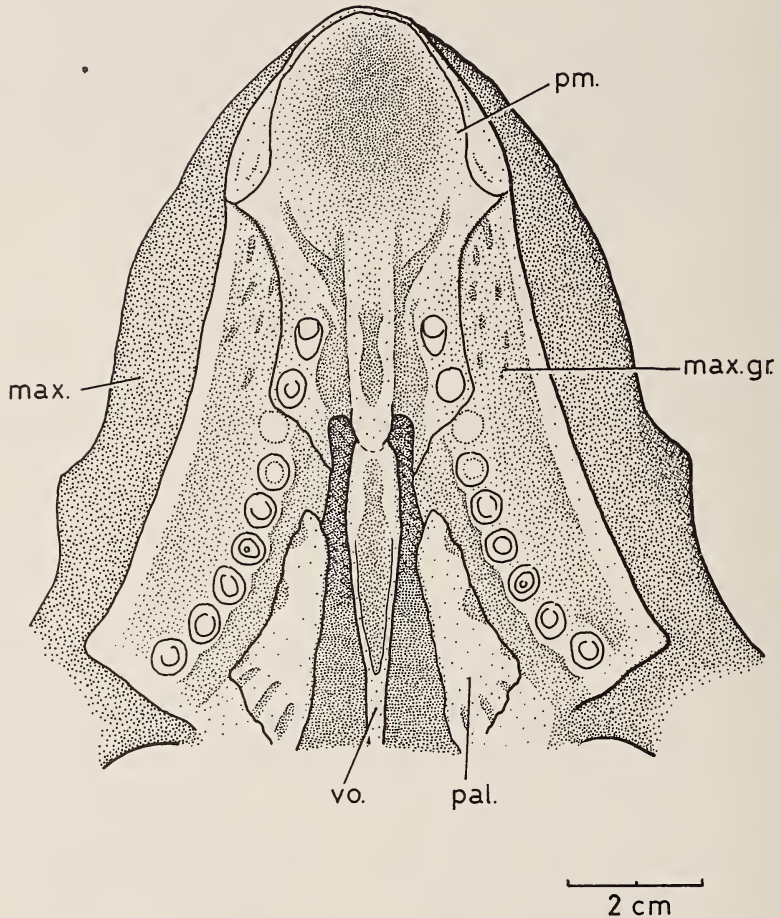


Fig. 9. *Endothiodon uniseriatus*. Type specimen BMNH 49414, from ?Beaufort West. Palatal view.

anteriorly, extending far back on to the internal surface of the pterygoid, but with little medial extension. Median ridge on posterior region of the pterygoids. Anterior pterygoid ramus very robust with modified lateral pterygoid process.

Anterior portion of the lower jaw toothless, prolonged into upward-curved and pointed beak fitting into vaulted palate. Dentary teeth long in a more or less straight line. Dorsal dentary trough lateral to tooth row. No dentary tables or lateral dentary shelf.

Genus *Pristerodon* Huxley, 1868Type species *Pristerodon mackayi* Huxley, 1868*Type material*

Skull and lower jaw BMNH R1810.

*Locality*

East London, Cape Province.

*Stratigraphic horizon**Cistecephalus* Zone.*Remarks on the type specimen*

The type specimen is a poorly preserved, incomplete skull and lower jaw in intractable matrix (Fig. 10). On the skull roof little, apart from the preparietal, parietal and postfrontal, can be made out. The pineal foramen is placed

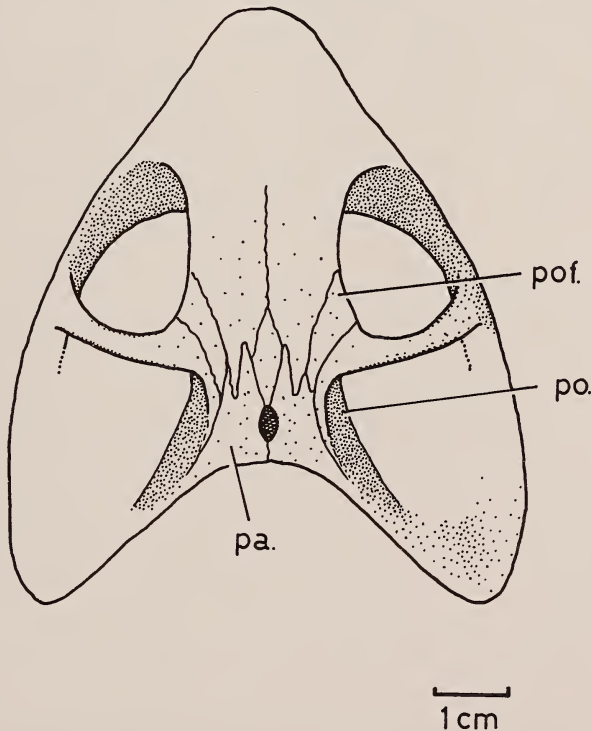


Fig. 10. *Pristerodon mackayi*. Type specimen BMNH R1650, from East London. Reconstructed dorsal view of skull.

relatively far back in the skull roof, and the preorbital region appears to have been fairly long. The intertemporal region is wide and formed mainly by the parietals. Canine tusks are absent.

Altogether nine small teeth are visible in the lower jaw. All the teeth are damaged and serrations are not visible.

Since the type specimen is so poorly preserved other species presently assigned to the genus were examined with a view to establishing a fuller generic diagnosis.

#### *Description of Pristerodon raniceps*

*P. raniceps* was described by Owen in 1876 as *Oudenodon raniceps*. It was referred to the genus *Pristerodon* by Broom (1915) on the basis of the presence of postcanine teeth. The type specimen consists of a skull and lower jaw (BMNH R1650) from East London (Fig. 11). While the bone is moderately well preserved, few sutures can be made out with certainty. The preparietal bone can be distinguished, and the pineal foramen is situated far back in the skull as in the type specimen of *P. mackayi*. The intertemporal region is broad, as in *P. mackayi*, and presumably formed mainly by the parietal bones. The palate is obscured by extremely hard matrix.

The lower jaw shows several important features. There is a broad lateral dentary shelf directly above the mandibular fenestra extending forward on the side of the dentary well beyond the anterior border of the fenestra. Six, possibly seven, posteriorly serrated teeth are visible in the jaw and are placed medially to a deep, thin-walled groove or sulcus in the dorsal edge of the dentary.

#### *Description of Pristerodon whaitsi*

*P. whaitsi* was described by Broom (1911) and is based on a skull (AMNH 5507) from Lemoenfontein, Beaufort West. The skull is laterally compressed and much of the dorsal skull roof in the interorbital and snout region is missing (Fig. 12). In the intertemporal region the parietals are widely exposed between the postorbitals and a postfrontal bone is present. The palate has suffered lateral distortion but certain features are nevertheless clear. The palatine bone is large, leaf-like and lies as a posterior extension of the premaxillary-maxillary secondary palate. Five small teeth are present medial to the canine tusk and lie in a straight line leading from an anterior medial position to a lateral position in line with the canine tusk. The posterior teeth in the row are situated on a platform of the maxilla, slightly lower than the level of the palatine and medial to the alveolar border. The posterior postcanine teeth lie close to the alveolar border.

In the lower jaw at least six functional teeth are present in a single row medial to a trough or sulcus in the dorsal border of the dentary. A large lateral dentary shelf is present and resembles that seen in *P. raniceps*.



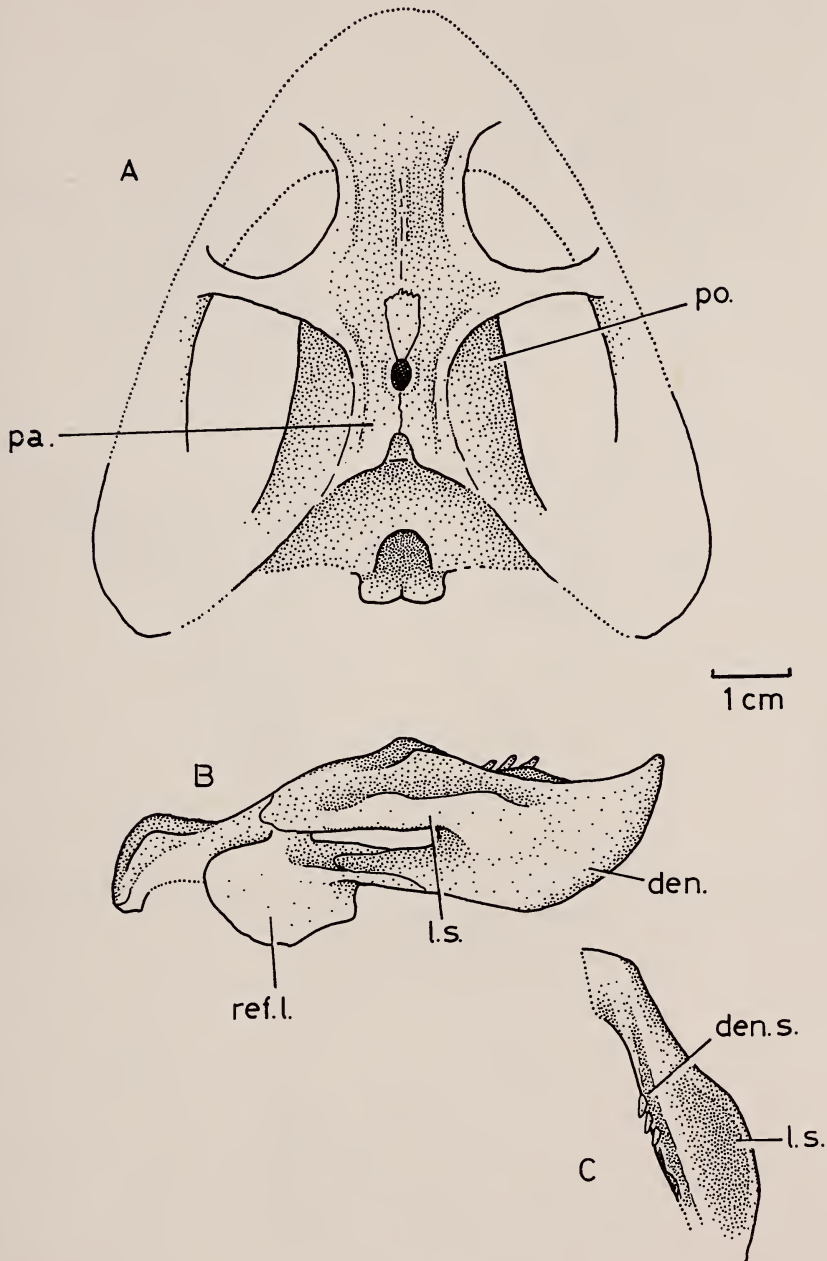


Fig. 11. *Pristerodon raniceps*. Type specimen BMNH R1650, from East London. A. Reconstructed dorsal view of skull. B-C. Lower jaw in lateral and dorsal views respectively.

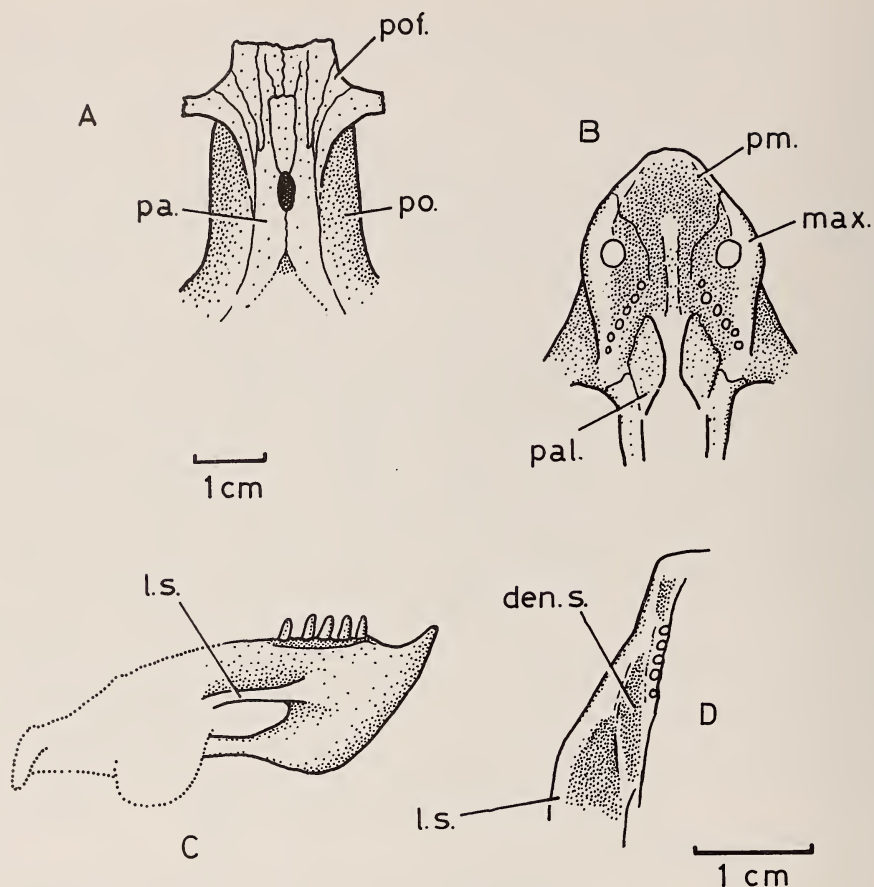


Fig. 12. *Pristerodon whaitsi*. Type specimen AMNH 5507, from Lemoenfontein, Beaufort West. A. Skull roof. B. Reconstructed palatal view. C-D. Lower jaw in lateral and dorsal view respectively.

### Diagnosis

Formulation of a diagnosis for the genus *Pristerodon* is made difficult by the nature of the type specimen of *P. mackayi* in which only a minimal amount of morphological detail is visible. Ideally, in order to draw up a full generic diagnosis, it would be necessary to include additional specimens firmly assigned to the same species but yielding more morphological information. Unfortunately such specimens are not available, although type specimens of other species at present assigned to the same genus are available (Fig. 13). If the information from the type species and additional species is pooled, then a diagnosis can be formulated, but at the risk of including characters that may have only specific significance. The alternative is to declare the type a *nomen nudum* and to base the genus on the earliest described, best preserved speci-

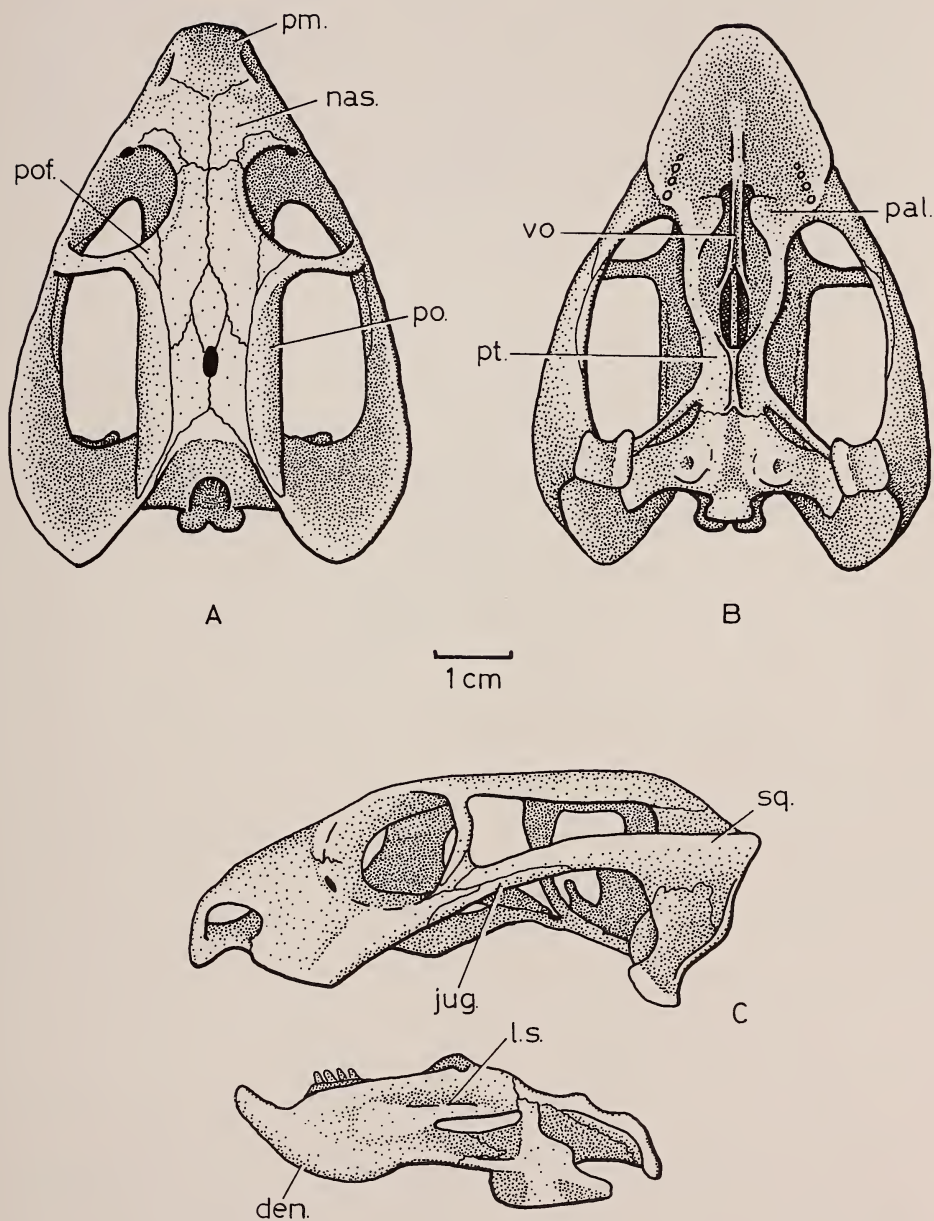


Fig. 13. *Pristerodon* sp. SAM-10153, from Dunedin, Beaufort West. A-B. Skull in dorsal and ventral views. C. Skull and lower jaw in lateral view.

men. In the interests of nomenclatural stability this alternative has not been followed here and it is proposed instead that *P. mackayi* remain the type species, and that the generic diagnosis be supplemented with information from the species *P. raniceps* and *P. whaitsi*. Where the characters included in the diagnosis are from either of the latter two species, the characters do not conflict with the condition found in *P. mackayi*, if verifiable. Any characters chosen that cannot be verified in the type species will be allowed to stand until it can be shown that the type species differs from the additional species in those characters.

This procedure has been explained in some detail since it is used elsewhere in the present work.

The revised generic diagnosis is as follows.

Small dicynodonts, with or without maxillary tusks. Intertemporal part of the skull roof broad, with wide parietal exposure. Palatines large and leaf-like, forming posterior extension of secondary palate surface. Interpterygoidal vacuity extending forward as a trough on to the rear of the vomerine septum. Median interpterygoid ridge continues anteriorly on to the ventral surface of the anterior pterygoid process. Palatal rim unbroken by notches or embayments anterior to the tusk position. Postcanine teeth lie in an oblique row medial to a deep sulcus in dorsal edge of dentary. Dentary carries strong lateral dentary shelf above and in front of mandibular fenestra.

Genus *Tropidostoma* (Seeley, 1889)

Type species *Tropidostoma microtrema* (Seeley, 1889)

*Type material*

Occiput and part of skull roof, BMNH R868.

*Locality*

Tafelberg, Beaufort West, Cape Province.

*Stratigraphic horizon*

*Cistecephalus* Zone.

*Remarks on the type specimen*

*Dicynodon microtrema* was described by Seeley in 1889, based on the occiput and posterior part of the skull roof of BMNH R868 (Fig. 14B).

In the same paper Seeley also described *Tropidostoma dunnii*, the posterior part of a skull (BMNH R866). From the description this appears to differ from *Dicynodon microtrema* mainly in the configuration of the lateral extension of the squamosal. In *Tropidostoma dunnii* it extends vertically above the level of the postparietal region, while in *D. microtrema* the temporal region is high above the lateral extension.

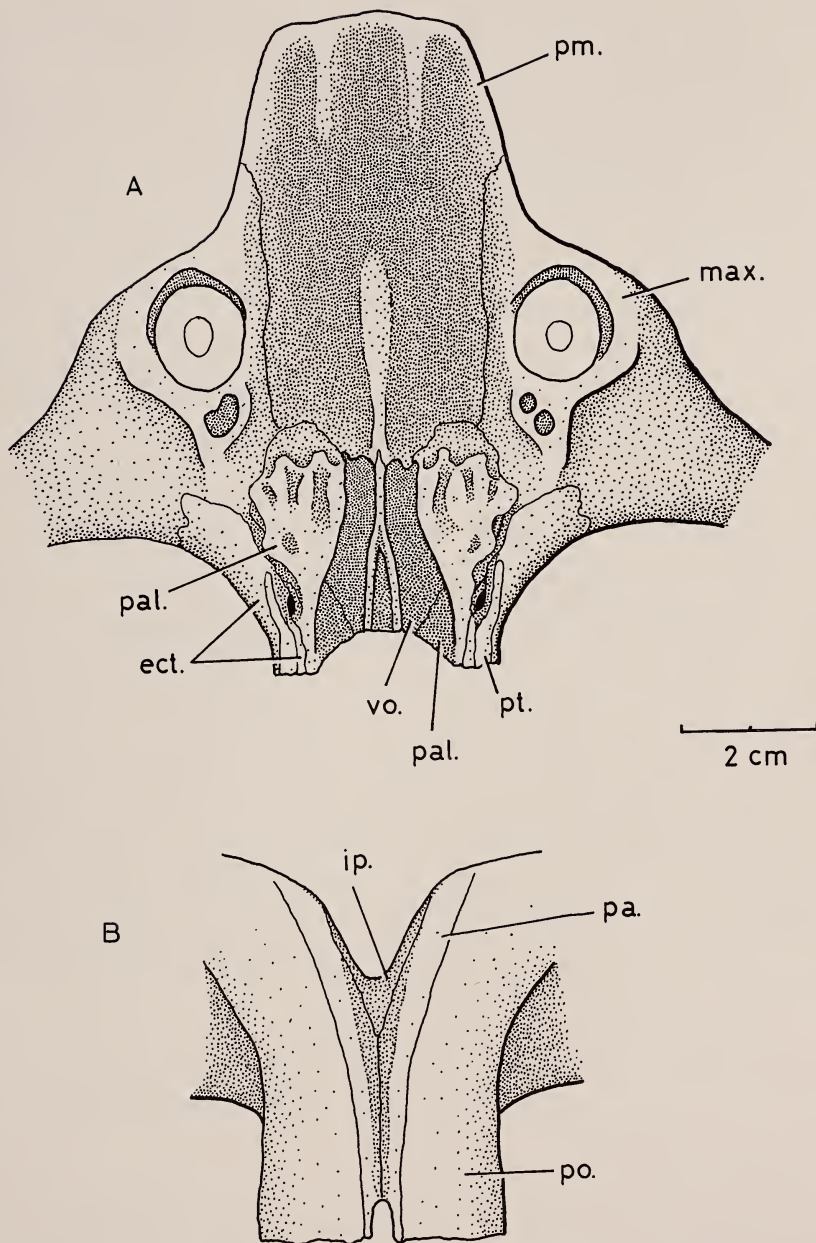


Fig. 14. A. *Tropidostoma microtrema*. BMNH R860, from Tafelberg, Beaufort West. Palatal view of specimen, showing empty sockets for postcanine teeth. B. *Tropidostoma microtrema*. Type specimen BMNH R868, from Tafelberg, Beaufort West. Dorsal view of the intertemporal region.

Broom (1915) referred new specimens from the Tafelberg locality to Seeley's *Dicynodon microtrema*. He found the new specimens to be characterized by the presence or absence of tusks (possibly a sexually dimorphic feature) and by small molars, which may be lost with age, behind the tusks or caniniform processes.

Broom considered that, since no *Dicynodon* specimen had postcanine teeth, the present forms should be referred to a new genus. He argued that *D. microtrema* was probably synonymous with *Tropidostoma dunni*, and therefore assigned the new Tafelberg specimens, as well as *D. microtrema*, to *T. microtrema*. One of the new specimens, BMNH R860 (Fig. 14A), formed the basis of Broom's description of *T. microtrema*: palatal premaxillary ridges are present; the postcanine teeth on the maxilla are striated; the septomaxilla lies within the nostril; the nasals bear thickened nasal bosses; the postorbitals and parietals are developed into a pair of lateral crests with a groove between them; the palatal portion of the premaxilla is large; the lower border of the prevomer is developed as a pair of ridges; and the palatines are large.

Re-examination of this specimen by the present authors showed that the 'prevomer lower border plates' actually represent the sides of a trough in the ventral edge of the vomerine septum, and that a sharp crest is present posterior to the tusk or caniniform process.

Broom (1932) discussed *Tropidostoma microtrema* and again drew attention to the encroachment of the postorbitals on the parietals, and the deep furrow present between the upper edges of the parietals behind the pineal opening. Broom's figure shows a trough in the ventral edge of the vomer.

In Watson's (1948) description of *Tropidostoma* he mentioned three ridges on the palatal part of the premaxilla and a canine tusk and two small circular postcanine teeth on each side. The anterior part of the palatine extends towards the midline and was described as being relatively small, although his figure 13 shows it to be extensive. A long interpterygoidal vacuity is shown. Watson's specimen (D. M. S. Watson Collection R48) has an associated lower jaw. The dorsal surface of the dentary was described as being divided into three grooves, but the two outer grooves are actually shallow troughs borne on dentary tables. Watson noted a groove in the upper surface of the dentary ramus and five teeth in a single series lying lingual to the dentary groove.

Additional undescribed material has been examined by the present authors. BMNH R6963, a specimen of *Tropidostoma* sp. with a lower jaw associated, shows a dentary table bearing a shallow trough, a dentary groove or sulcus with teeth lying in a row lingual to the sulcus, and a deep median symphyseal trough (Fig. 15).

SAM-10681, a skull of *Tropidostoma* sp., shows a pinched intertemporal region with a furrow between the parietals, tusks, small nasal bones, nostrils placed high in the snout, a crest on the alveolar border posterior to the tusk, postcanine teeth posterior to the tusk and situated close to the alveolar border, a short vomerine trough, large palatines, and a long interpterygoid vacuity.

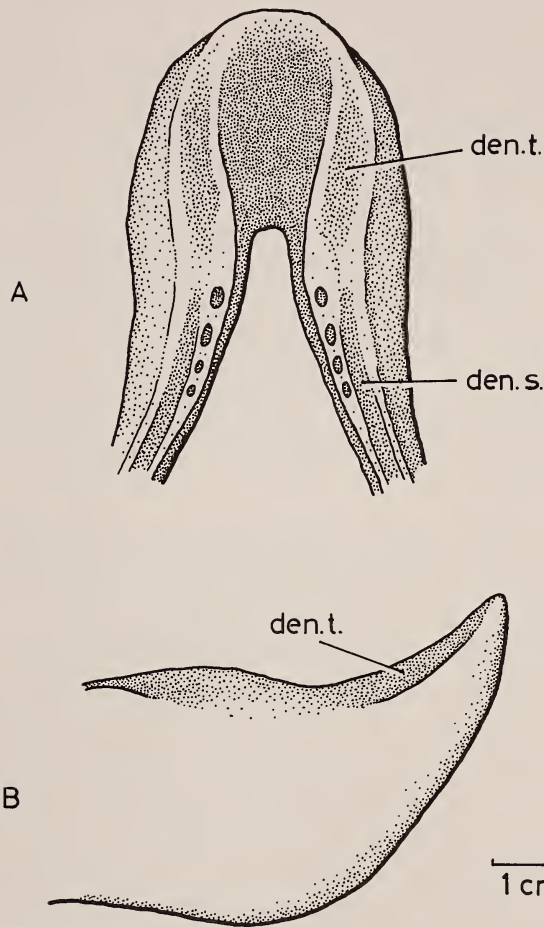


Fig. 15. *Tropidostoma* sp. BMNH R6963. A-B. Anterior portion of lower jaw in dorsal and lateral views.

For the present it is felt justifiable to include information from all the above specimens in a generic diagnosis.

#### *Diagnosis*

Medium-sized dicynodonts with or without tusks. Alveolar border behind tusk or caniniform process forms a sharp postcanine crest that may or may not bear teeth. Palatine large with bulbous anterior palatal portion. Vomer bears trough (which may be short) along ventral edge. Interpterygoidal vacuity long. Nostril set high in the snout. Nasals bear weak bosses. Pinched intertemporal

region. Postorbitals overlie parietals and form sides of a deep groove or furrow leading backward from the pineal foramen.

Lower jaw with weak dentary tables. Dorsal surface of dentary table bears trough. Deep median trough between dentary tables. Dentary sulcus present. Few postcanine teeth present in a row in longitudinal groove lingual to dentary sulcus. Weak lateral dentary shelf.

#### *Related genera*

Keyser (1973) redescribed *Cteniosaurus platyceps* Broom and assigned it to *Tropidostoma microtrema*. The characters that Keyser regarded as common to the two forms are a similar configuration of the bones of the skull surface, and the nostril placed high in the skull. Other similarities that can be detected are: weak nasal bosses, a long interpterygoidal vacuity, a few small postcanine teeth, a sharp postcanine crest, and extensive palatines that have an inflated posterior part and a smooth anterior part that meets the premaxilla.

A very weathered jaw ramus is the only lower jaw material available for *Cteniosaurus*.

Unlike previously described material that has been assigned to *Tropidostoma*, *Cteniosaurus* has a wide intertemporal region. This is not pinched and does not show the deep median furrow leading backward from the pineal foramen. In this respect it resembles specimens such as the type specimen (SAM-2356) of *Dicynodon rogersi* Broom & Haughton, 1917, and a similar as yet undescribed specimen SAM-B390, which have postcanine teeth but wide intertemporal regions. It is considered here that the state of the intertemporal region is a meaningful character since its morphology will impose constraints on the organization of the jaw musculature. It is therefore felt that *Cteniosaurus* should not be included in the genus *Tropidostoma*. Both *Tropidostoma* and *Cteniosaurus* may be regarded as early *Oudenodon*-like forms, which in some cases retain postcanine teeth. Features such as the weak nasal bosses, the long interpterygoidal vacuity, the sharp postcanine crest, and the shape of the palatine all ally *Cteniosaurus* and *Tropidostoma* with *Oudenodon* (see p. 223).

Although *Tropidostoma*, *Cteniosaurus*, and *Oudenodon* are clearly related, it is not possible at this stage to determine the exact relationships of the three genera.

#### Genus *Rhachiocephalus* (Owen, 1876)

Type species *Rhachiocephalus magnus* (Owen, 1876)

#### *Type material*

Incomplete skull BMNH 36252.

#### *Locality*

Brak River, Fort Beaufort, Cape Province.



*Stratigraphic horizon**Cistecephalus* Zone.*Remarks on the type specimen*

Seeley (1898) erected the genus *Rhachiocephalus* for *Oudenodon*-like (i.e. tuskless) forms with a narrow intertemporal region. *Oudenodon magnus* Owen, 1876, was made the type species and transferred to the genus *Rhachiocephalus*.

The type specimen is tuskless and fairly large (skull length approximately 50 cm). Nasal bosses are present. The intertemporal region is narrow and drawn up into a crest and the parietals are only slightly exposed on the skull roof. The pineal foramen is situated in the middle of a bony boss. Few details of the palate can be distinguished, but it is possible that an interpterygoidal crest exists. There is a median palatal premaxillary ridge and the palatines are large. In describing the same specimen in 1932, Broom notes that there are no postfrontal bones.

*Remarks on other species*

Two additional species of *Rhachiocephalus* have been described. *R. angusticeps*, described by Broom (1937), is an incomplete skull in the Transvaal Museum (no. 1489). The skull is large and tuskless, has a narrow intertemporal region with a crest and a pineal foramen situated in a bony boss. The description given by Broom does not permit closer comparison, but there seem to be no obvious features separating *R. angusticeps* and *R. magnus* at either the generic or specific level. Since the aim of the present work is to attempt to formulate generic diagnoses, not to revise dicynodonts at the specific level, for the moment both species will be allowed to stand.

*Rhachiocephalus dubius* (SAM-11313) from the Luangwa Valley, Zambia, was described by Boonstra (1938). Although the type specimen has a narrow intertemporal region, re-examination shows that this form is tusked. There is no pineal boss, instead the skull roof in this region is shallowly concave. There are nasal bosses, but these are very elongate, and may have been affected by crushing.

Since *R. dubius* does not show two of the main characteristics expected in the genus *Rhachiocephalus*, namely tusklessness and a pineal boss, it cannot remain in that genus. Keyser & Cruickshank (1979) make *R. dubius* the basis of their new genus *Odontocyclops*. This will be discussed later (p. 238), when it will be argued that certain of the large tusked forms, amongst them '*Odontocyclops dubius*', may simply be larger members of one of the *Dicynodon* species such as *D. leoniceps*.

*Diagnosis*

Large tuskless dicynodonts. Nasal bosses present. Intertemporal region narrow and drawn up into a crest. Parietals hardly exposed on skull roof. Pineal

foramen situated in a bony boss. Median palatal premaxillary ridge. Palatines large. No postfrontal bones.

Genus *Eocyclops* Broom, 1913

Type species *Eocyclops longus* Broom, 1913

*Type material*

Skull in AMNH.

*Locality*

Grootvlei, Paardekraal, Beaufort West, Cape Province.

*Stratigraphic horizon*

*Cistecephalus* Zone.

*Remarks on type specimen*

As described by Broom (1913), *Eocyclops longus* shows the following features: skull length is approximately 44 cm; nasal bosses are present; smaller bosses are present over the orbits; the large pineal foramen is surrounded by the thickened, ring-like parietal; the preparietal is absent; the postfrontal extends along the postorbital bar; the postorbitals almost overlap the parietals in the intertemporal region; tusks are absent; there is a feeble caniniform process.

Broom (1913) considered that *Oudenodon magnus* Owen, 1876, belonged to the new genus, but it was later found to possess a preparietal. *O. magnus* eventually became the genotype for *Rhachiocephalus*, as described above.

From the published descriptions the only feature that separates *Rhachiocephalus* and *Eocyclops* is the apparent lack of a preparietal in the latter. This may be an unreliable feature for taxonomic purposes, as frequently it is difficult to interpret the sutures around or within the pineal boss. Haughton (1917), in describing what he considered to be a specimen of *Eocyclops longus* with a preparietal, obviously set little store on this as a distinguishing feature. (Even so, Broom later reassigned this specimen to a new genus, *Megacyclops*.) A specimen in the University Museum, Oxford (TSK 23), which is undoubtedly *Eocyclops*, shows a ring-like preparietal surrounding the pineal foramen. However it is evident that this bone is the preparietal only because the specimen is broken through the pineal foramen and sutures are clearly visible. It is possible, therefore, that Broom mistook a ring-like preparietal for the parietal.

Until the type specimen of *Eocyclops longus* can be re-examined in detail it cannot be stated with confidence whether a preparietal is present or not. However, in view of other similarities it is considered here that, even if a preparietal is absent from the skull roof, this is not a character that necessitates generic separation, and it is recommended that *Eocyclops longus* be accommodated in the genus *Rhachiocephalus*.

Genus *Platycyclops* Broom, 1932Type species *Platycyclops haughtoni* Broom, 1932*Type material*

Skull SAM-8750.

*Locality*

Doornplaas, Graaff-Reinet, Cape Province.

*Stratigraphic horizon**Cistecephalus* Zone.*Remarks on the type specimen*

Broom described *Platycyclops haughtoni* in 1932 from a large, moderately flat skull without tusks. The preorbital region is wide. There are large postorbitals and narrow parietals. The preparietal is crescentic and forms the front half of a pineal boss.

Broom stated that a postfrontal is not present although Haughton & Brink (1954) stated correctly that there is a very large and distinct postfrontal.

The type specimen was re-examined and the following additional information gained. The pineal foramen faces anterodorsally. Behind it there is some parietal exposure, but the postorbitals close over the parietals posteriorly. As preserved, the intertemporal region is wide and flat because the postorbitals, instead of sloping ventrolaterally, face directly dorsally. This could be due in part to post-mortem deformation.

The jugal has a short spur, which extends up into the postorbital bar. There are small nasal bosses. The nostril is recessed with a definite posterior margin and does not grade imperceptibly into the surface of the snout. The postfrontal extends along the postorbital bar.

On the palate there is a strong postcaniniform crest. There are two anterior palatal premaxillary ridges and a median posterior ridge. The vomer does not bear a trough along its ventral edge and there is a fairly short interpterygoidal vacuity. The palatines have a large bulbous anterior exposure.

Other features are as Broom described them, except that a postfrontal is present.

*Remarks on other species*

Broom (1940) described two additional species of *Platycyclops*, *P. latirhinus* and *P. rubidgei*. These conform to Broom's diagnosis of the genus but show some variation in the intertemporal region. In *P. latirhinus* this region is moderately wide, although the parietals are still overlapped by the postorbitals to a great extent. In *P. rubidgei* the intertemporal region is narrower. Such variation is probably tolerable within a species, almost certainly within a genus, since the important diagnostic feature here is whether the parietals are overlap-

ped by the postorbitals, forming a structure approaching a sagittal crest. Absolute width is probably diagnostically unimportant, as it may vary with absolute skull size. The degree to which overlapping occurs may be age- or sex-dependent, leading to the variation seen.

In *P. pricei* (Broom & George 1950) the postorbitals approach each other over the parietals, although they do not meet. In *P. acutirostris* (Broom & George 1950) the postorbitals meet over the parietals.

In other features these four specimens conform to the generic description.

There seems to be little in Broom's original description to warrant erecting a new genus for these forms apart from the condition of the preparietal—absent in *Eocyclops*, present in *Platycyclops*. However, this distinction becomes irrelevant in the present work since *Eocyclops* has been referred to the genus *Rhachiocephalus* where the preparietal is quite similar to that of *Platycyclops*. It is therefore recommended that *Platycyclops* also be included in the genus *Rhachiocephalus*.

#### Genus *Neomegacyclops* Boonstra, 1958

Type species *Neomegacyclops whaitsi* (Broom, 1931)

#### *Type material*

Part of the skull roof, postorbital bar and part of the zygoma SAM-3425.

#### *Locality*

Graaff-Reinet, Cape Province.

#### *Stratigraphic horizon*

Uncertain.

#### *Remarks on the type specimen*

In 1917 Haughton described a partial dicynodont skull that, although possessing a preparietal, he considered to be sufficiently similar in other respects to *Eocyclops longus* to be included in that genus and species. The preparietal of the specimen forms most of a boss round the pineal foramen. The parietals have a very small exposure between the overlapping postorbitals. There is a small nasal boss and a thickened postfrontal. Haughton reported that there was no septomaxilla showing on the surface of the snout. The reconstructed length of the skull would be approximately 50 cm.

Broom (1931) renamed the specimen *Megacyclops whaitsi* because the pineal opening is small and the preparietal and parietal form a huge, rounded pineal boss. Boonstra (1953) subsequently erected the new genus *Neomegacyclops* for the specimen since the name *Megacyclops* was found to be preoccupied.

Re-examination of the type specimen reveals few other features of diagnostic significance since the palate is unprepared. The nostril has a definite

posterior margin. The orbit is triangular and the postfrontal extends into the postorbital bar. On the ventral surface of the distal part of the postorbital bar there is a smooth recess that seems to be continuous with a smooth recess on the posterior dorsal surface of the suborbital bar. These may be for muscle attachment, in which case the extension of the postfrontal into the postorbital bar may be a means of strengthening it or its connection with the skull roof.

Another specimen, SAM-K1393, has certain features in common with *Neomegacyclops whaitsi* and the other tuskless forms described above. There is a boss mostly posterior to the pineal foramen formed by the parietals. A preparietal is present. The postorbitals overlap the parietals closely in the intertemporal region. There are nasal bosses and prefrontal thickenings. There is a median crest on the nasal and frontal bones, but this may be the result of lateral compression. The nostril has a definite posterior margin. The postfrontal extends into the postorbital bar. There is a recess on the ventral surface of the distal part of the postorbital bar and also on the posterior dorsal surface of the suborbital bar. The jugal forms part of the posterior surface of the postorbital bar.

Additional features of this specimen are a median interpterygoid crest, absence of a vomerine trough, absence of tusks, a sharp postcaniniform crest and a palatine with a bulbous anterior portion.

It has not been possible to find any features in the type specimen of *Neomegacyclops whaitsi*, or in a related species *Neomegacyclops rugosus* (Haughton 1932), or in the specimen SAM-K1393 described above that would debar any of these forms from the genus *Rhachiocephalus*. It is therefore suggested that these forms should be included in that genus.

*Note on the large tuskless dicynodonts*

The genus *Rhachiocephalus* is considered to be a well-defined, distinct taxon. The genera *Eocyclops*, *Platycyclops* and *Neomegacyclops* are synonymous with *Rhachiocephalus*. *Peloro-cyclops* (Broom 1932) and *Kitchingia* (Broom & George 1950), which are not discussed here, can probably also be accommodated within this genus.

Genus *Oudenodon* Owen, 1860

Type species *Oudenodon baini* Owen, 1860

*Type material*

Skull lacking lower jaw, BMNH 36232.

*Locality*

Near Fort Beaufort, Cape Province.

*Stratigraphic horizon*

Uncertain.

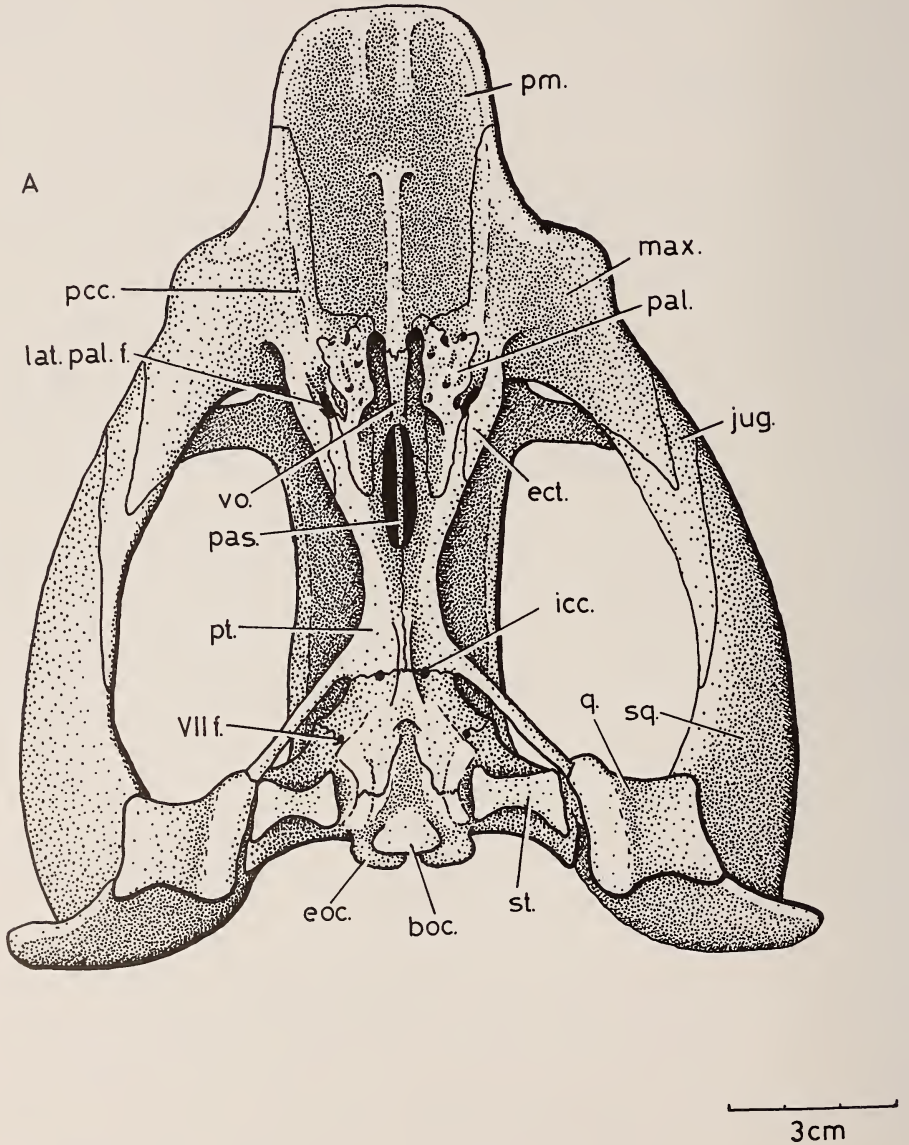


Fig. 16. *Oudenodon baini*. Type specimen BMNH 36232, from 'near Fort Beaufort'. Skull in ventral view.

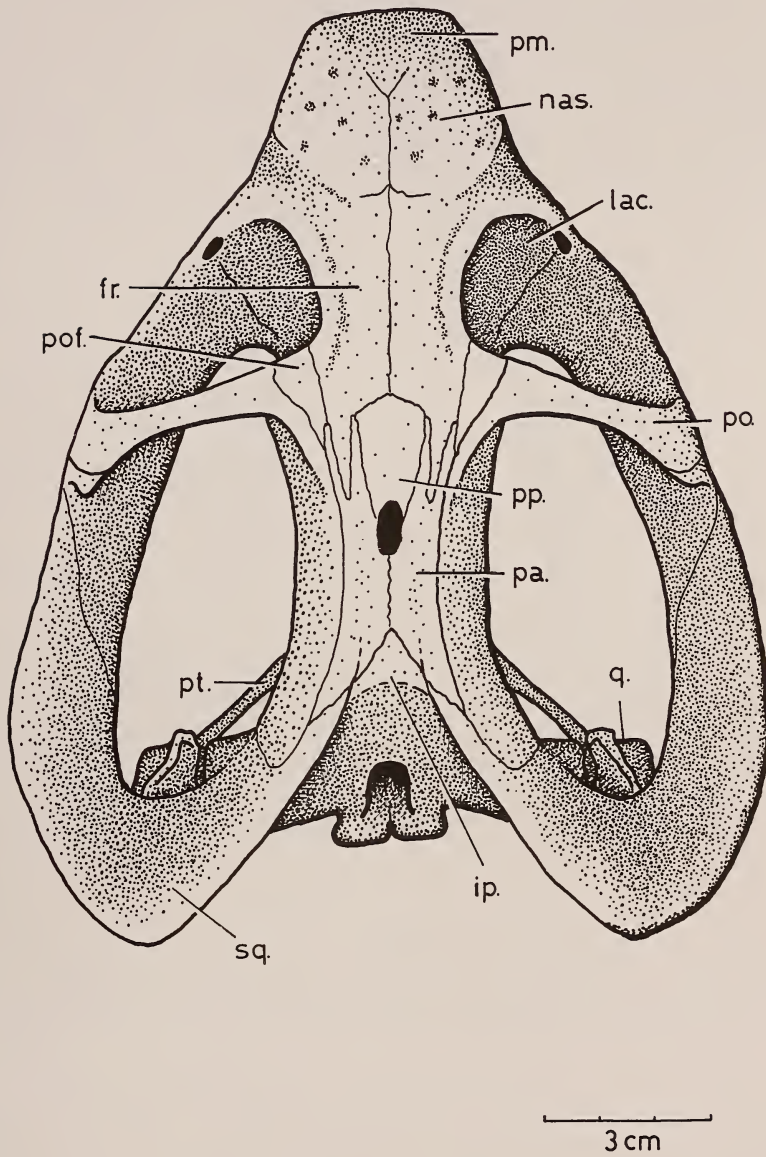


Fig. 17. *Oudenodon baini*. Type specimen BMNH 36232. Skull in dorsal view.

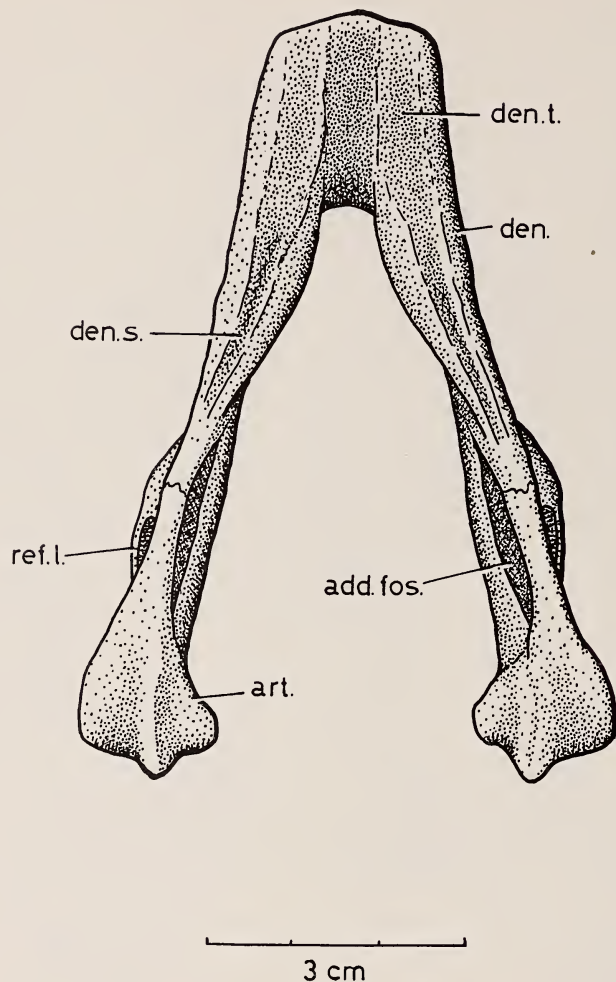


Fig. 18. *Oudenodon* sp. SAM-6045, from Houd Constant, Graaff-Reinet. Lower jaw in dorsal view.

### *Diagnosis*

The genus *Oudenodon* (Figs 16–18) has recently been reviewed and illustrated by Cluver & Hotton (1981) and their diagnosis with slight modification will be used here.

Medium-sized to large dicynodonts (skull length ranging from 100 mm to over 300 mm). Teeth lacking in both upper and lower jaws. Postorbitals well separated on skull roof by parietals. Septomaxilla recessed within external



naris, lacrimal in some species extends forward above maxilla to posterior margin of naris. Nasal forms boss over naris. Maxilla carries weak caniniform process, with sharp-edged posterior crest. Palatal part of palatine divided into an inflated posterior area, and a smooth anterior part that meets the premaxilla. Vomers form short septum in anterior part of interpterygoidal fossa. Ectopterygoid large with palatal exposure, pterygoid does not contact maxilla. Dentaries with narrow dentary tables, dorsal edge of dentary with deep sulcus. Dorsal process on rear of dentary weak or absent. Weak lateral dentary shelf above large mandibular fenestra.

Genus *Aulacephalodon* (Owen, 1844)

Type species *Aulacephalodon baini* (Owen, 1844)

*Type material*

Skull BMNH 36238.

*Locality*

Fort Beaufort, Cape Province.

*Stratigraphic horizon*

Uncertain.

*Note on the spelling of generic name*

Seeley (1898) originally erected this taxon as a subgenus of *Dicynodon* with the following spelling: *Aulacephalodon*. Broom (1932) raised the subgenus to the generic level and for no apparent reason changed the spelling to *Aulacocephalodon*. Both Keyser (1969) and Tollman & Grine (1980) have discussed the validity of this and conclude that *Aulacephalodon* is the correct generic name; this will be used here throughout.

*Remarks on the type specimen*

In 1898 Seeley erected the subgenus *Aulacephalodon* for members of the genus *Dicynodon* (i.e. tusked forms) that were broad headed and short snouted. *Dicynodon baini* Owen, 1844, became the type species of the new genus.

*Aulacephalodon baini* is described by Owen (1844, 1876) as a skull slightly wider than long with a wide intertemporal region and exposed parietals. The pineal foramen is surrounded by a boss. The postorbitals in the intertemporal region are steep sided and there is a boss on the posterior surface of the postorbital bar. Tusks are present. The anterior pterygoid rami are widely divergent.

The snout and palate are not well preserved in the type specimen and little detail can be made out. In his *Catalogue* Owen (1876) also described *Dicynodon tigriceps*, which Seeley later assigned to *Aulacephalodon*. This specimen

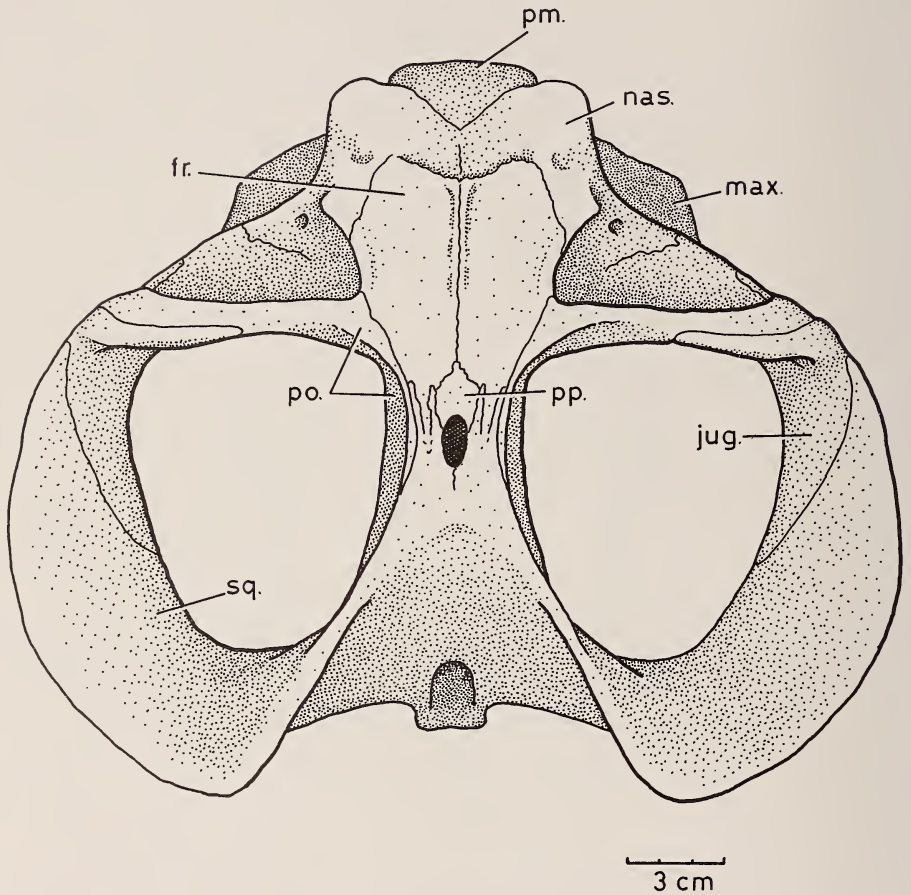


Fig. 19. *Aulacephalodon laticeps*. Type specimen AMNH 5564, from Grootvlei, Beaufort West. Skull in dorsal view.

(BMNH 36235) is better preserved and, in addition to the features described above, it has prefrontal and nasal bosses, a ridge across the snout between the prefrontal bosses, and a boss on the jugal of the zygoma, lying just posterior to the postorbital bar. These features cannot be verified on the more poorly preserved *A. baini*. The postorbital boss is not present in *A. tigriceps* and may therefore represent a specific feature of *A. baini*, so this feature should not be included in a generic description of *Aulacephalodon*. Otherwise these features

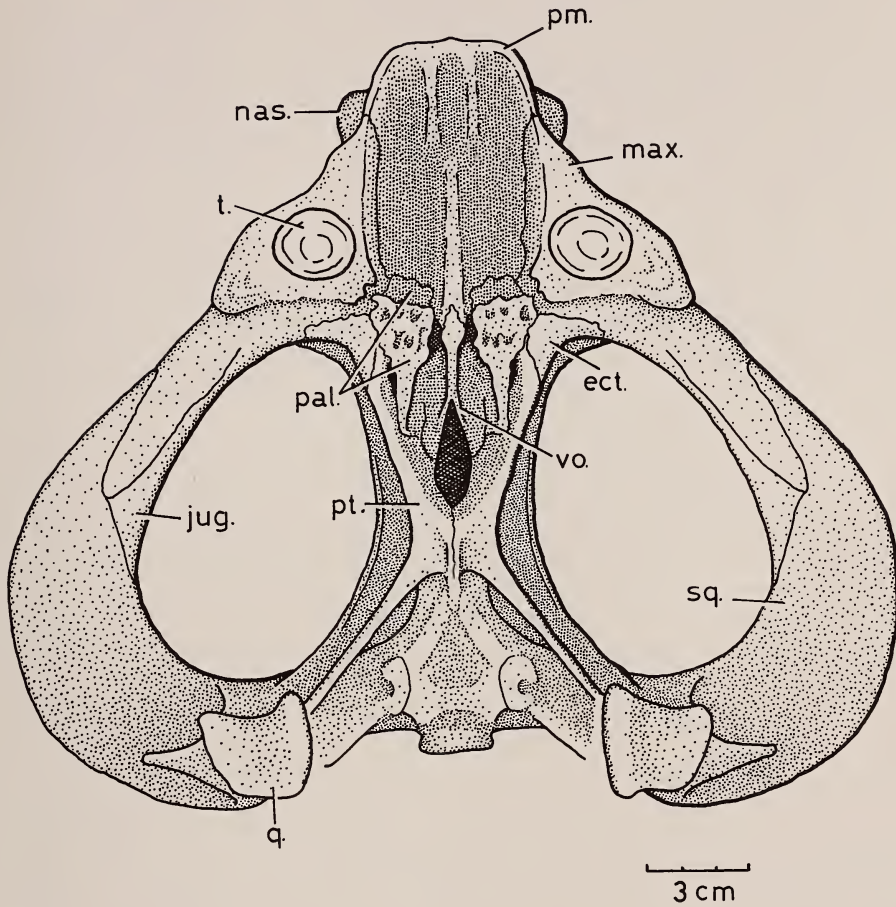


Fig. 20. *Aulacephalodon laticeps*. Type specimen AMNH 5564. Skull in ventral view.

may be combined to give a generic diagnosis of *Aulacephalodon*.

Various other species have been assigned to the genus (see Haughton & Brink 1954). In a recent review Keyser (1972) concluded that so-called specific differences are actually due to age and he considered that most of the species may be invalid. In their study on a large sample of *Aulacephalodon* skulls, Tollman, Grine & Hahn (1980) concluded that biometrical (allometric) methods indicate that only one species (*Aulacephalodon baini*) was present during the southern African Permian, and that this species showed clear sexual dimorphism and ontogenetic variation.

*Description of additional material*

The type specimen of *Aulacephalodon luckhoffi* Broom, 1937 (SAM-K1231) is the greater part of a skull lacking the lower jaw. It is in a reasonable state of preservation. In this specimen the skull is slightly longer than wide, but otherwise all diagnostic characters named above are present. In addition, *A. luckhoffi* shows a steep postorbital region that is drawn up into a low dorsal ridge. The postorbital overhangs the side wall of the braincase and forms a well-defined recess beneath the skull roof. The boss on the zygoma is well marked. The nostril is deeply recessed and has a definite posterior margin. The postfrontal bone is absent. A ridge on the premaxilla runs from the postero-dorsal corner of the nostril to the maxillary rim. There is a moderately large interpterygoid vacuity. The median vomerine plate does not bear a trough. The palatines are extensive and have an anterior bulbous portion. There are two anterior premaxillary palatal ridges as well as the single posterior premaxillary palatal ridge. There is no postcaniniform crest.

The type specimen of *Aulacephalodon laticeps* (Broom, 1912) (AMNH 5564) is another good skull (without the lower jaw) in which the palate has been prepared recently (Figs 19-20). This specimen shows all the features described above, where verifiable, with only some minor modifications such as the prefrontal boss being weak. In addition, *A. laticeps* exhibits a jugal that bears a high process abutting against the postorbital posteriorly and extending far up the postorbital bar. There is also a relatively prominent interpterygoid crest.

Several undescribed specimens in the South African Museum (SAM-10053, SAM-10021 and SAM-K6064) have been examined and found to exhibit all characters noted above wherever the material permits investigation.

SAM-K6064 has a lower jaw *in situ*. This specimen is well preserved but unprepared. However, the form of the lower jaw is apparent. The dentary symphysis is massive and very deep. Posterior to the symphysis the depth of the jaw decreases to approximately one-third that of the symphysis. A typical dicynodont lower jaw condyle is present. At approximately one-third of the length of the jaw from the anterior end a lateral dentary shelf arises. Its length is also approximately one-third the length of the jaw. The shelf is directed ventrally so that it occludes the mandibular fenestra. A dorsal dentary sulcus is present.

*Diagnosis*

If the information from the foregoing specimens is pooled in the manner described earlier (p. 212) the following diagnosis can be formulated.

Medium-sized, tusked dicynodonts with a wide intertemporal region. Parietals exposed on skull roof. Pineal foramen surrounded by a boss. Postorbitals in intertemporal region steep sided and drawn up into ridge dorsally. Postorbitals overhang side wall of braincase forming recess beneath skull roof on each side. Boss on jugal of zygoma. Jugal has tall, dorsal process extending far

up postorbital bar. Prefrontal and nasal bosses. No postfrontal bone. Nostril is deeply recessed and has a definite posterior margin. Ridge on maxilla posterior to nostril.

Interpterygoidal vacuity moderately long. Ventral edge of vomerine plate without trough. Palatines bulbous. No postcaniniform crest.

Massive dentary symphysis with dentary tables. Lateral dentary shelf occludes mandibular fenestra. Dentary sulcus present.

#### *Related genera*

It may be possible to refer *Digalodon* (Broom & Robinson 1948) to this genus. This is based on a small specimen that generally conforms to the generic diagnosis except that the maxillary rim is cut upward in front of the canine tusk. It may prove to be either a distinct genus closely related to *Aulacephalodon* or a distinct species of that genus.

#### Genus *Pelanomodon* Broom, 1938

Type species *Pelanomodon rubidgei* Broom, 1938

#### *Type material*

Skull, Rubidge Collection 10.

#### *Locality*

Kareelaagte, Graaff-Reinet, Cape Province.

#### *Stratigraphic horizon*

*Daptocephalus* Zone.

#### *Remarks on the type specimen*

In Broom's (1938) original description, *Pelanomodon rubidgei* is characterized by the absence of tusks, the saddle-backed skull with beak folded down on the rest of the skull, the marked upwardly directed nasal bosses, smaller horn-like bosses on the prefrontals, little trace of a postfrontal, the small boss on the postorbital bar, the small preparietal almost entirely in front of the pineal foramen, the broad, flat parietals that produce the wide intertemporal region, and the large squamosals which flare out posterodorsally.

#### *Remarks on additional specimens*

In the same publication Broom (1938) mentioned *Aulacephalodon moschops* and considered that, since it was tuskless, it ought to be placed in another genus. Haughton & Brink (1954) assigned it to *Pelanomodon*.

*Pelanomodon moschops* (AMNH 5325, Figs 21-22) has the following features in addition to those described above: the postorbital in the intertemporal region is steep sided, there is a ridge across the snout between the prefrontal bosses, there is a smoothly recessed nostril, a labial fossa is present,

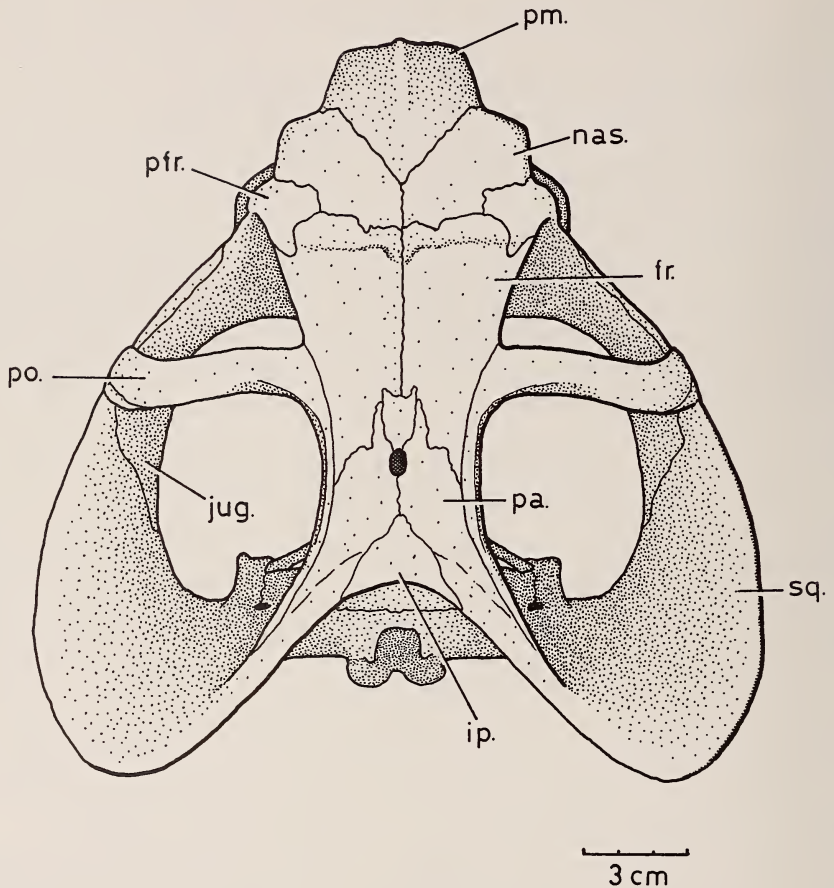


Fig. 21. *Pelanomodon moschops*. Type specimen AMNH 5325, from Oudeberg, Graaff-Reinet. Skull in dorsal view.

the interpterygoidal vacuity is relatively short, the palatines are large and the anterior portion is not bulbous but slopes slightly to meet the premaxilla, a very slight postcaniniform crest is present, the jugal boss, vomerine trough and interpterygoid crest are all absent.

A lower jaw for *Pelanomodon* is not known.

#### Diagnosis

Taking into account features from the above specimens, the following diagnosis may be formulated.

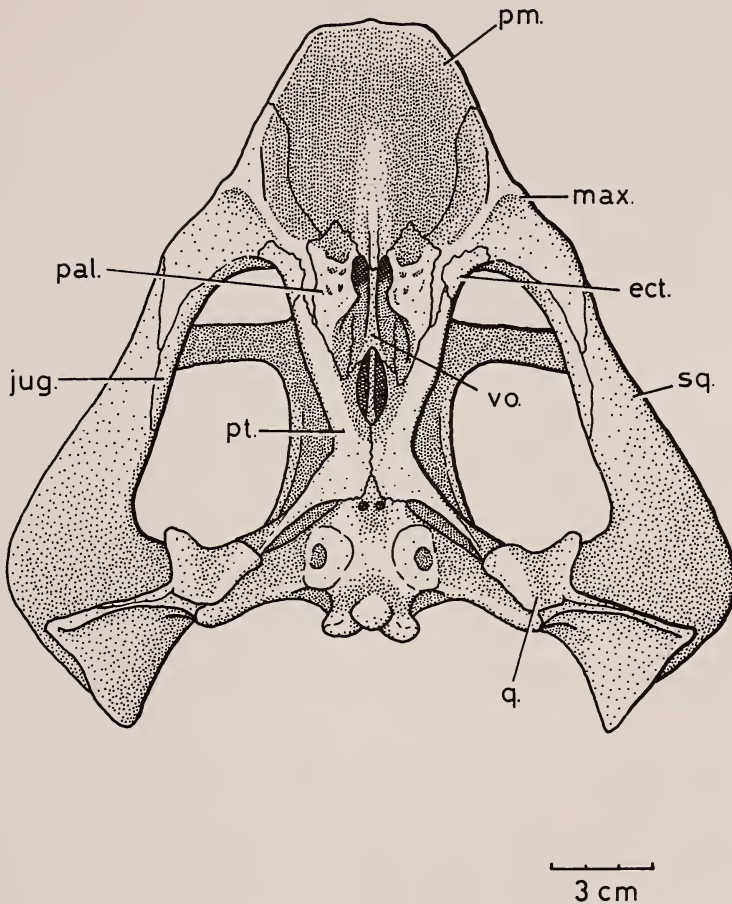


Fig. 22. *Pelanomodon moschops*. Type specimen AMNH 5325. Skull in ventral view.

Medium-sized dicynodonts without tusks. Wide intertemporal and interorbital regions. Snout bent downward on nasals, which are bent downward on rest of skull. Postorbital in intertemporal region steep sided. Ridge across snout between prefrontals. Small prefrontal bosses, larger nasal bosses. No (or reduced) postfrontal bone. No jugal boss. Unbroken palatal rim. Smoothly recessed nostril. Labial fossa present. Relatively short interpterygoid vacuity. No anterior palatal ridges. Large palatines not bulbous but sloping forward to meet premaxilla. No vomerine trough. Very slight postcaniniform crest.

#### *Related genera*

*Aulacephalodon* and *Pelanomodon* have many features in common, but also some important differences: *Pelanomodon* has a smoothly recessed nostril,

lacks an interpterygoid crest, has a palatine that slopes forward, and lacks anterior palatal ridges, whereas *Aulacephalodon* has a deeply recessed nostril, a palatine with an anterior bulbous portion, anterior palatal ridges, and an interpterygoid crest.

These features and the rarity of *Pelanomodon* specimens relative to *Aulacephalodon* argue against *Pelanomodon*'s being merely the female of *Aulacephalodon*, although it is possible that *Pelanomodon* specimens have been misidentified in the past. Both *Dicynodon sidneyi* Broom, 1940, and *D. locusticeps* Huene, 1942, are probably members of *Pelanomodon*, the former being a small member of the genus.

Keyser (1972) considers that the similarities between the two genera are the result of a similar biting mechanism, both forms possibly feeding among vegetation in shallow water.

It is considered here that *Pelanomodon* and *Aulacephalodon* are closely related genera that should be kept separate, at least for the present, until more of the tuskless forms can be investigated.

#### Genus *Dicynodon* Owen, 1845

Type species *Dicynodon lacerticeps* Owen, 1845

#### *Type material*

Skull and lower jaw BMNH 36233.

#### *Locality*

Tarka prolongation of the Winterberg, Cape Province.

#### *Stratigraphic horizon*

Uncertain.

#### *Diagnosis*

The genus *Dicynodon* (Figs 23–26) has recently been revised and illustrated by Cluver & Hotton (1981) and their diagnosis with slight modification will be used here.

Medium-sized to large dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Palatal rim sharp edged, uninterrupted by notch. Palatal portion of palatine large and flat, making short contact with premaxilla. Vomers form long, narrow septum in interpterygoidal fossa. Anterior border of interpterygoidal fossa formed by a crest that joins the vomerine septum. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basisoccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow



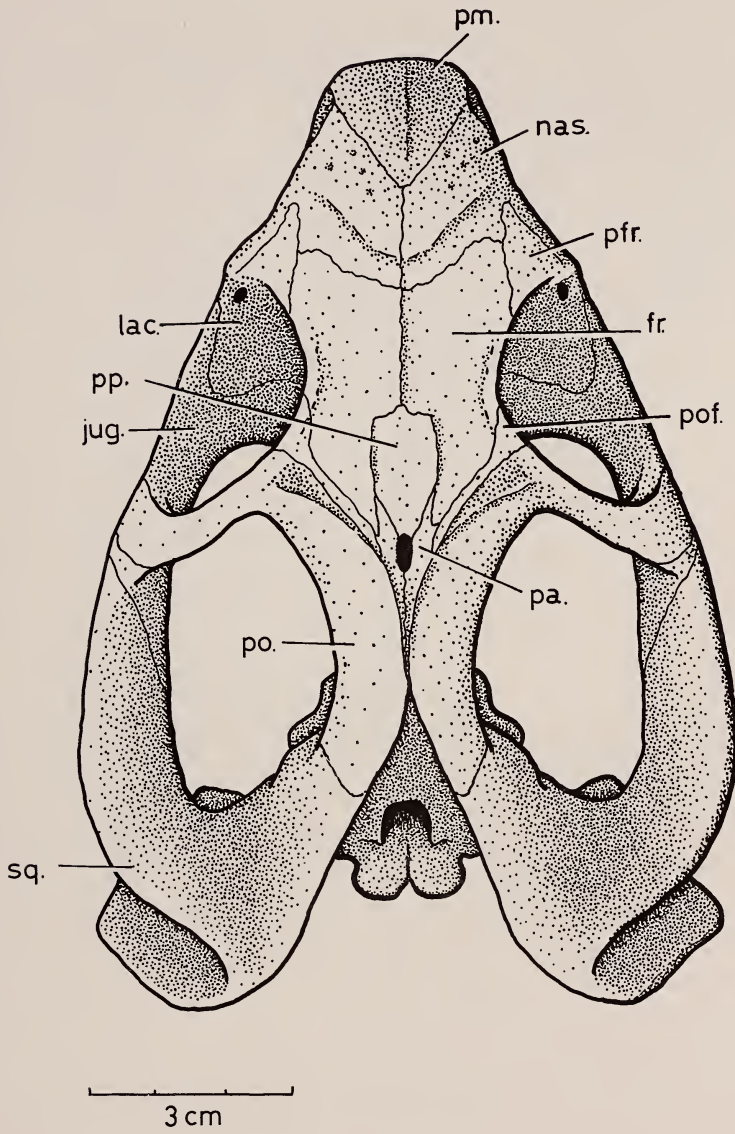


Fig. 23. *Dicynodon* sp. SAM-B88, from Hoeksplaas, Murraysburg. Skull in dorsal view.

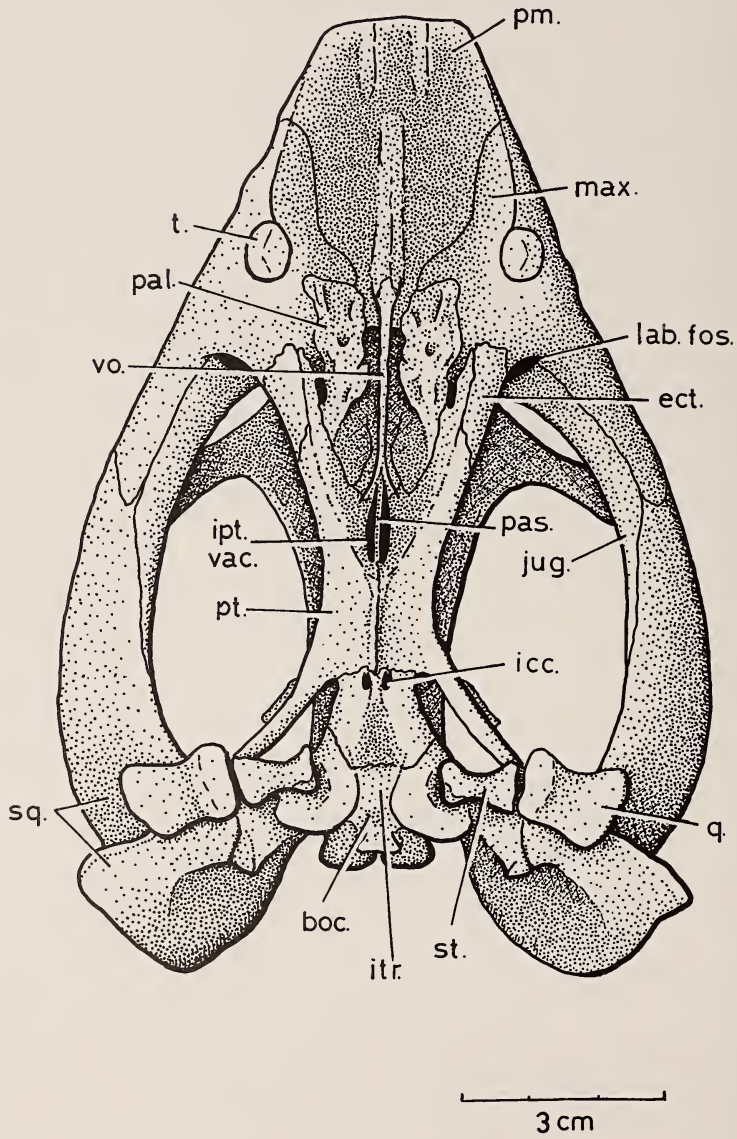


Fig. 24. *Dicynodon* sp. SAM-B88. Skull in ventral view.

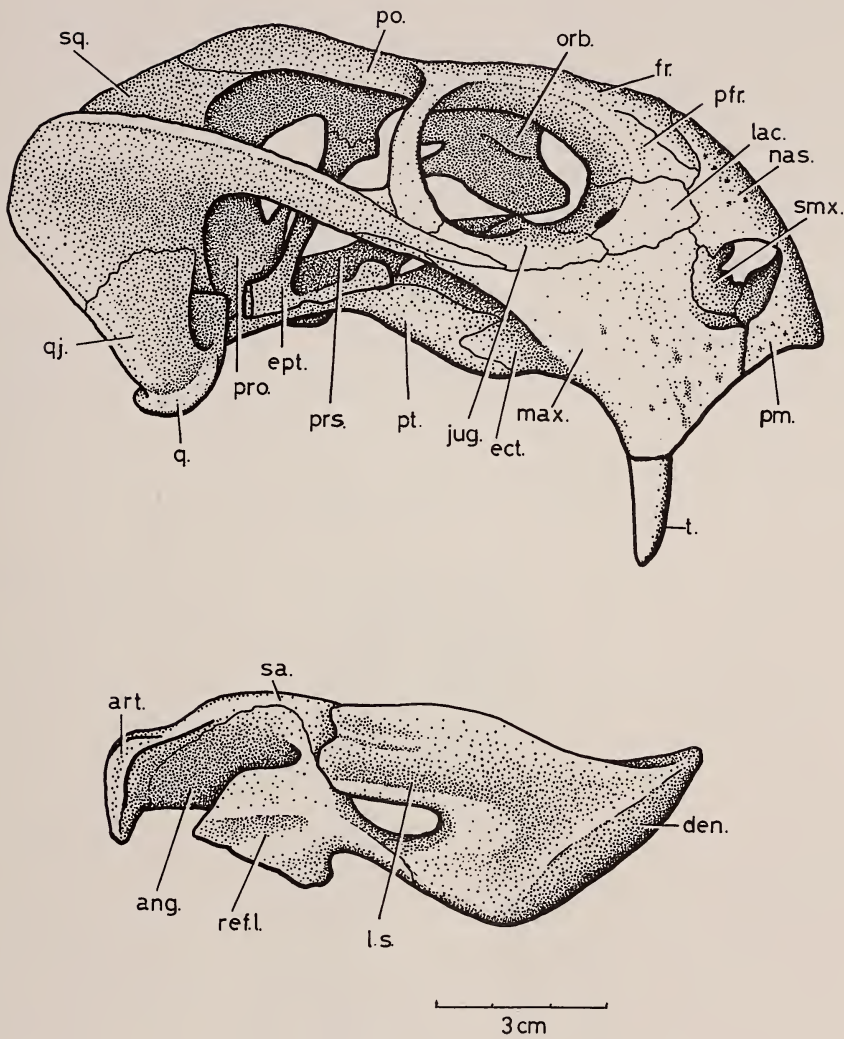


Fig. 25. *Dicynodon* sp. SAM-B88. Skull and lower jaw in lateral view.

dentary tables. Dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak posterodorsally directed process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf. Occipital surface of opisthotic carries depression above paroccipital process.

*Note on the large tusked dicynodonts*

Several large tusked dicynodonts have been described in the literature, not only members of the genus *Dicynodon* but also of *Dinanomodon* (Broom 1938) and *Odontocyclops* (Keyser & Cruickshank, 1979). Such forms are characterized by a narrow intertemporal region where the postorbitals overlap the parietals to some degree, absence of a pineal boss, absence of a postcaniniform crest (where it is possible to investigate this feature), and the presence of tusks. In some forms (*Dicynodon njalilus* and *Dinanomodon* spp.) the postorbitals meet over the parietals, obliterating their exposure on the skull roof. In these forms the pineal opening is reduced to a very narrow slit, which does not seem to be the result of lateral compression since the basicranial axis shows no signs of deformation.

It is possible that all these forms are simply large members of a species of *Dicynodon* such as *Dicynodon* (previously *Daptocephalus*) *leoniceps* (Cluver & Hotton 1981). The palatal structure is quite consistent with this. It is possible that the very close overlap of the postorbitals in some forms may be related to large size or advanced age.

The genus *Odontocyclops* was erected by Keyser & Cruickshank (1979) who considered it to be related to *Dicynodon leoniceps* and *Dinanomodon* by the following features that few other Permian dicynodonts share: a small posteriorly placed interpterygoid vacuity with raised margins, an anterior process of the footplate of the epipterygoid, a large posterior extension of the premaxilla in the secondary palate, reduction of the ectopterygoid, a high position in the snout of the external nostril, contact between the maxilla and septomaxilla, the small pineal foramen, and absence of a pineal boss.

In fact, most of these features are widespread in the genus *Dicynodon* and do not serve to

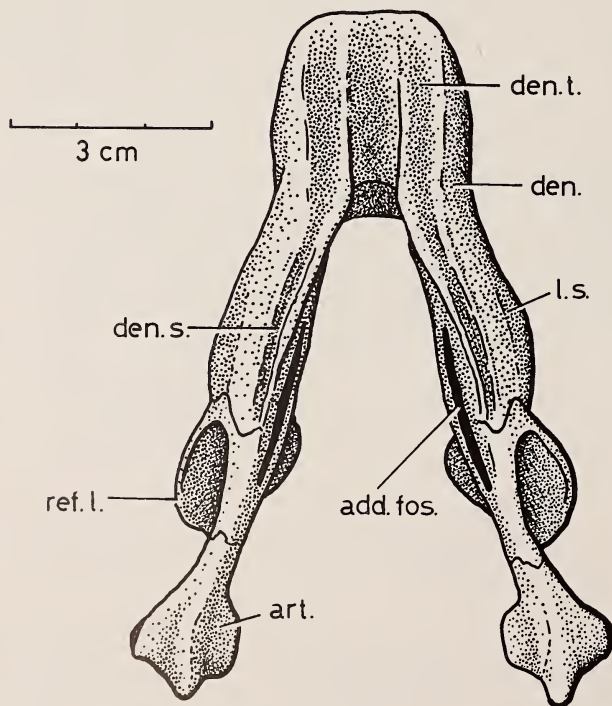


Fig. 26. *Dicynodon* sp. SAM-B88. Lower jaw in dorsal view.

separate the three forms mentioned above from other members of that genus. For example, *Dicynodon* sp. SAM-B88 (Cluver & Hotton 1981) shows all the above features.

The anterior process of the footplate of the epipterygoid is not a feature that is particularly useful for taxonomic purposes since the ossification of this process is very variable; however, judging from the groove present on the lateral surface of the pterygoids, an extension of the footplate was present in most Permian forms (including *Eodicynodon*) whether cartilaginous or bony.

Keyser & Cruickshank (1979) distinguish *Odontocyclops* from the other two related genera, *Daptocephalus* (i.e. *Dicynodon leoniceps* of our classification) and *Dinanomodon* on the following features: the concavity of the dorsal snout surface, the broad intertemporal region, and large size. These features are used to demonstrate that *Odontocyclops* cannot be ancestral to the long-snouted Triassic forms with a crested intertemporal and, while this may be so, nevertheless there is nothing in this character suite that debars *Odontocyclops* from the genus *Dicynodon*. The intertemporal region mentioned is broad relative to the Triassic forms, but it is not outside the range of variation tolerable within the genus *Dicynodon* and is shown by species such as *D. calverleyi* and *D. bathyrhynchus*.

In conclusion, it is proposed that large tusked forms such as *Odontocyclops* and *Dinanomodon* be accommodated within the genus *Dicynodon*, as they probably represent large members of a species such as *D. leoniceps* or are distinct but closely related species.

### Genus *Robertia* Boonstra, 1948

Type species *Robertia broomiana* Boonstra, 1948

#### *Type material*

Skull SAM-11761.

#### *Locality*

Klein Koedoeskop, Beaufort West, Cape Province.

#### *Stratigraphic horizon*

*Tapinocephalus* Zone.

#### *Remarks on the type specimen*

The genus is represented only by *Robertia broomiana*. The type specimen consists of most of a skull and lower jaw reasonably well preserved but embedded in an intractable matrix. Little preparation has been carried out.

The original description (Boonstra 1948) includes the following features: the skull is relatively broad with a maximum length of 80 to 100 mm; the snout is weak and short; the small nostril opens near the alveolar border; the interorbital width is less than the intertemporal width; the molar teeth are small, simple cones arranged in the lower jaw in a single fairly regular row along the lingual side of the dentary; the dentary teeth are 5 to 9 in number; and the upper postcanine teeth all lie on the maxilla posterolingual to the canine or caniniform process, forming an irregular group of one to eight.

The original description is based on several topotypes and referred specimens as well as the type specimen.

Toerien (1953) added a figure and described another specimen assigned to *Robertia broomiana*. He noted that the anterior ramus of the pterygoid bears a ridge continuous with the alveolar border.

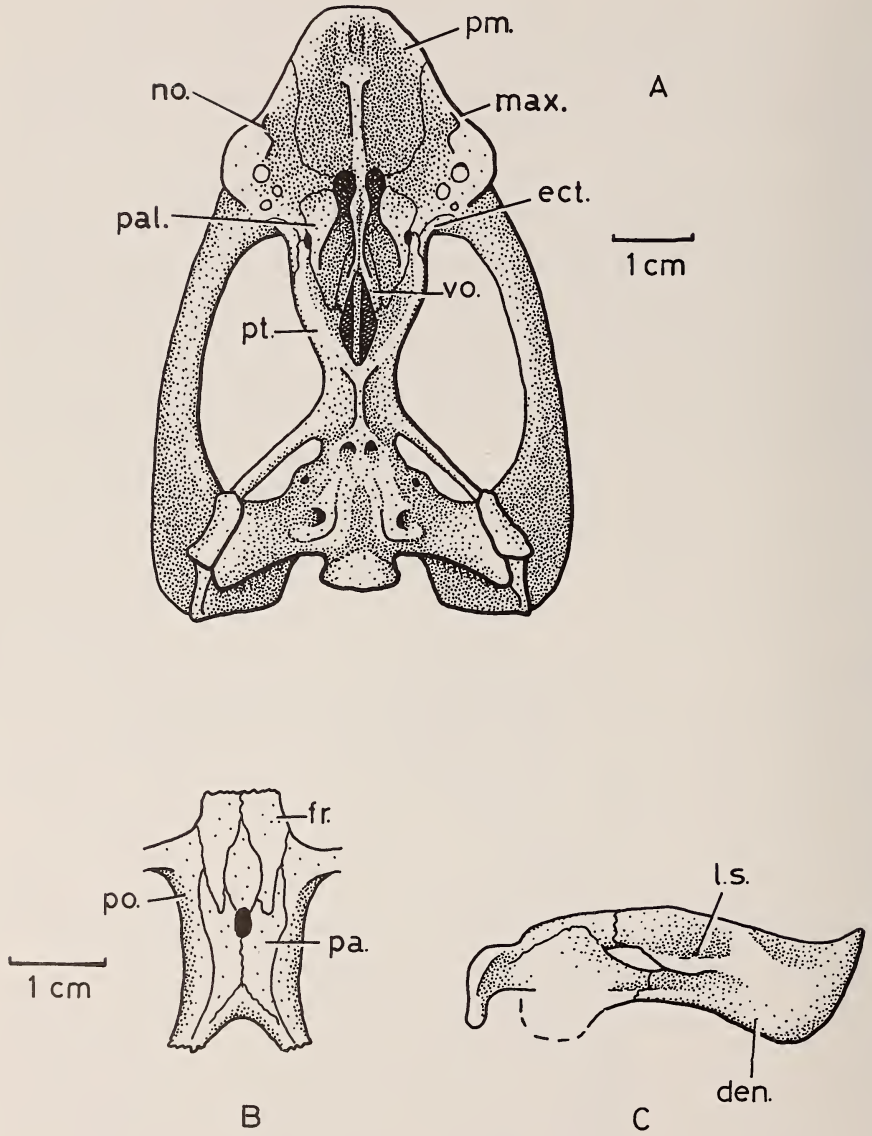


Fig. 27. A. *Robertia* sp. SAM-11461, from Buffelsvlei, Prince Albert. Skull in ventral view. B-C. *Robertia* sp. SAM-11885, from Michau's Request, Beaufort West. Skull roof and lower jaw.

*Description of additional specimens*

The following description is based on material in the South African Museum that can be assigned to the genus *Robertia* according to the description above. The specimens are SAM-11885 (Fig. 27B-C) from Michau's Request, Beaufort West, SAM-11890 from Skoorsteen, Laingsburg, SAM-K296 (Fig. 27A) from Die Krans van Tuinkraal, Beaufort West, and SAM-11451 from Buffelsvlei, Prince Albert.

A full description of *Robertia* does not exist at present in the literature, so a rather more detailed description than for other specimens is given here.

Skull length ranges between 60 and 100 mm. Tusks may or may not be present. The intertemporal and interorbital widths are approximately equal. The parietals are exposed behind the pineal foramen giving a moderately wide intertemporal region. The preorbital widths are approximately equal. The preorbital region is shorter than the length of the orbit. Unlike species of *Emydops* or *Pristerodon*, the maxillary rim is drawn down round the tusk or into the caniniform process.

A few (usually three) postcanine teeth are present on the maxilla in a more or less straight line posteromedial to the canine or caniniform process. Anterior to the canine or caniniform process there is a notch in the maxilla, which cuts back into the medial surface of the caniniform process or into the bone sheathing the tusk.

The palatine is of moderate size. It forms part of the surface of the secondary palate and is continuous horizontally with the premaxilla. The palatine approaches the vomer but does not make contact with it. Posterior to the level of the palatines, the ventral edge of the median plate of the vomers runs posterodorsally and bears a wide trough. The sides of the trough separate posteriorly to form the anterior border of the interpterygoid vacuity. A short median palatal ridge is present anteriorly where the median vomer plate meets the premaxilla.

The anterior rami of the pterygoids are strong. Posteriorly each ramus bears a high, sharp ridge. The ridges converge towards the midline where they fuse together and continue posteriorly as a single median ridge, which runs in the midline of the posterior part of the pterygoid and over the basisphenoid. A Y-shaped system of ridges therefore dominates the pterygoid-basisphenoid area of the palate.

The interpterygoid vacuity is moderately extensive. Its length is half that of the distance between its posterior edge and the anterior border of the choana.

The foramina for the passage of the internal carotid arteries are prominent. They are situated immediately behind the median pterygoid-basisphenoid ridge and face ventrally.

The quadrate bears a shallowly convex medial and lateral condyle. The lateral condyle is marginally the greater in area. The lower jaw is fairly robust with a sharp, squarish tip. Anteriorly it bears well-defined dentary tables on the

dorsal surface. A longitudinal dentary sulcus is not present on the dorsal surface of the jaw ramus.

A few small teeth are present on the dentary.

The lateral surface of the dentary is built up into a ledge approximately one-third of the length of the jaw. The ledge is directed ventrally so that its outer surface faces mostly laterally and so tends to occlude the mandibular fenestra. There are marked striations on the lateral surface of the dentary ledge.

The posterior part of the jaw is typically dicynodontian with a downwardly projecting retroarticular process and an elongate lateral articular condyle.

### *Diagnosis*

Taking into account the new material, the following generic diagnosis may be formulated.

Small to medium (up to 12 cm skull length) dicynodonts. Intertemporal region moderately wide and parietals exposed. Tusks present or absent. Maxillary rim extended ventrally round tusk or into caniniform process. Approximately three postcanine teeth arranged in a row in the maxilla. Notch present on the palatal surface of the maxilla. Palatine moderately large but does not reach the vomers. Y-shaped ridge dominates the pterygoids and basisphenoid. Trough on the ventral edge of the median plate of vomer. Dentary tables on lower jaw. A few small teeth present on the dentary. A lateral dentary shelf takes up the middle third of the length of the jaw and is directed ventrally so that it tends to occlude the mandibular fenestra.

### Genera *Brachyuraniscus* Broili & Schröder, 1935 and *Brachyprosopus* Olson, 1937

The taxonomic status of the following genera from the *Tapinocephalus* Zone of the Beaufort Group is enigmatic.

*Brachyuraniscus reuningi* was described by Broili & Schröder (1935) and two new species were added to the genus by Toerien (1953). The new species were *B. merwevillensis* and *B. broomi*, the latter a redesignation of *Brachyprosopus broomi* (Olson 1937). Toerien considered that *Brachyprosopus broomi* was so similar to *Brachyuraniscus* in palatal features that it should be included in the same genus. However, he overlooked the very different shape of the palatine in *Brachyprosopus* and the fact that this form apparently has a labial fossa.

The type specimens of both *Brachyuraniscus merwevillensis* and *reuningi* have been lost. The figures of *Brachyuraniscus merwevillensis* (Toerien 1953) do not allow much detail to be discerned, and those of *B. reuningi* show it to be a very incomplete specimen. It is felt, therefore, that no useful purpose is served in trying to establish the relationships of these two forms. It would seem, however, that *Brachyprosopus* is a distinct genus. It shows certain primitive features such as the short secondary palate, a number of well-



developed postcanine teeth, the wide intertemporal region with the parietals exposed, and features of the braincase, which Olson (1937) described. The presence of a labial fossa and the shape of the palatine in not encroaching upon the midline seem to be distinctive features. Even so, without further information, especially from the lower jaw, it is difficult to define the relationships of *Brachyprosopus* very accurately, and it is at present left *incertae sedis* as there is insufficient evidence to determine its taxonomic position.

Genus *Diictodon* Broom, 1913

*Diagnosis*

This genus has recently been reviewed by Cluver & Hotton (1981) and their diagnosis with minor modifications will be used here. (See Figs 28–30.)

Medium-sized dicynodonts (average skull length 110 mm), jaws either lacking teeth altogether or bearing a single pair of maxillary tusks. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla recessed within external naris, maxilla rises high on the side of the snout to meet nasal. Nasal forms boss over external naris. Maxilla carries a prominent caniniform process clearly demarcated from anterior palatal rim by a deep notch. Palatal portion of palatine small, does not meet premaxilla. Vomers form short septum in interpterygoid fossa. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries carry wide dorsal dentary tables, with high medial borders. Rear of dentary table extended medial to level of inner surface of jaw ramus. Dorsal edge of dentary rounded behind dentary table, no posterior dorsal process of the dentary present. Mandibular fenestra large, no expanded lateral dentary shelf for insertion of adductor musculature.

Genus *Emydops* Broom, 1912

Type species *Emydops minor* Broom, 1912

*Type material*

Skull and lower jaw AMNH 5525.

*Locality*

Kuilspoort, Beaufort West, Cape Province.

*Stratigraphic horizon*

*Cistecephalus* Zone.

*Remarks on the type specimen*

The skull and jaw are obliquely crushed and the snout badly damaged (Fig. 31C). The skull roof behind the snout region is exposed and sutures can be distinguished. Teeth are not visible although Broom (1913) stated that, having broken the specimen through, he could see 'at least two small teeth'. When

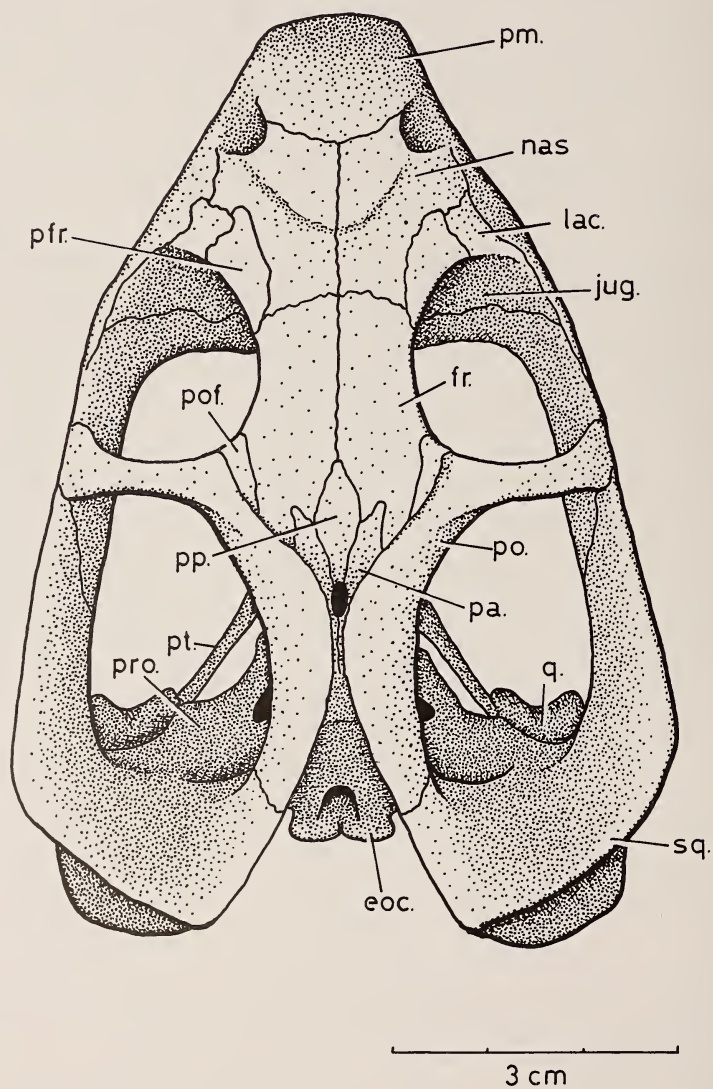


Fig. 28. *Diictodon* sp. SAM-10086, from Dunedin, Beaufort West. Skull in dorsal view.

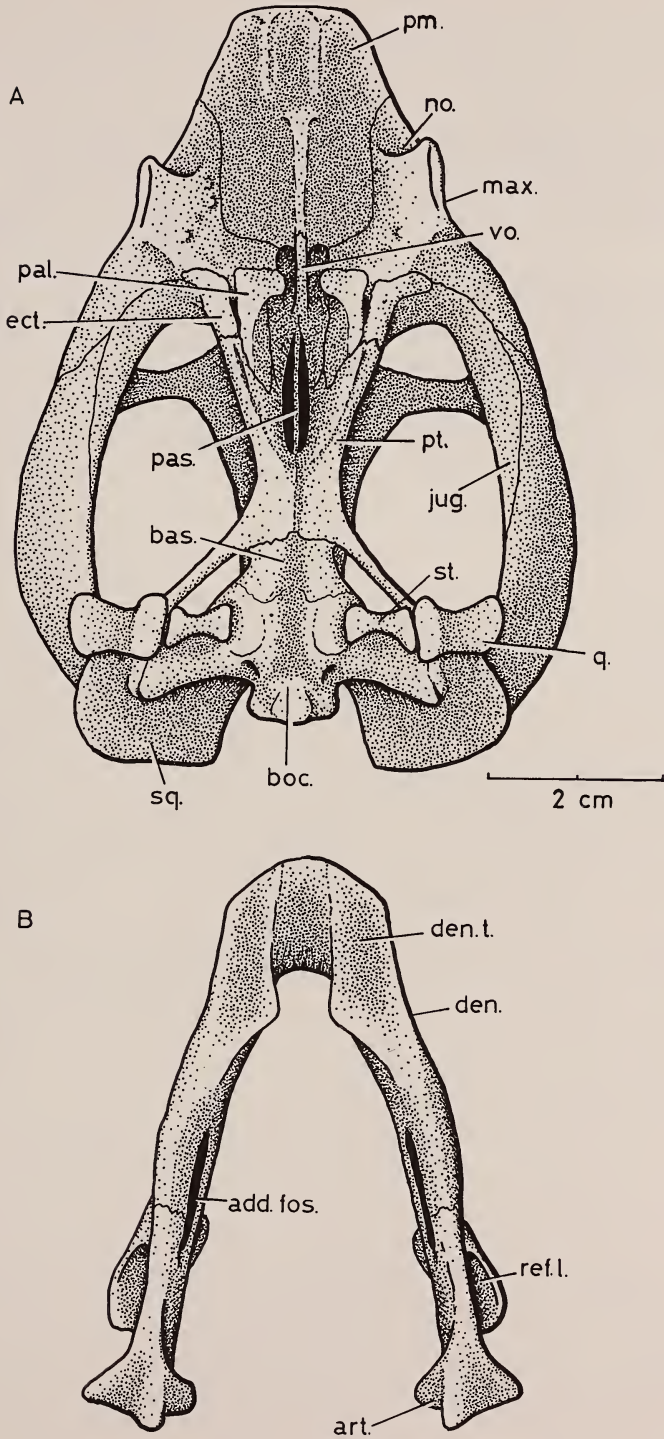


Fig. 29. *Diictodon* sp. SAM-10086. A. Skull in ventral view. B. Lower jaw in dorsal view.

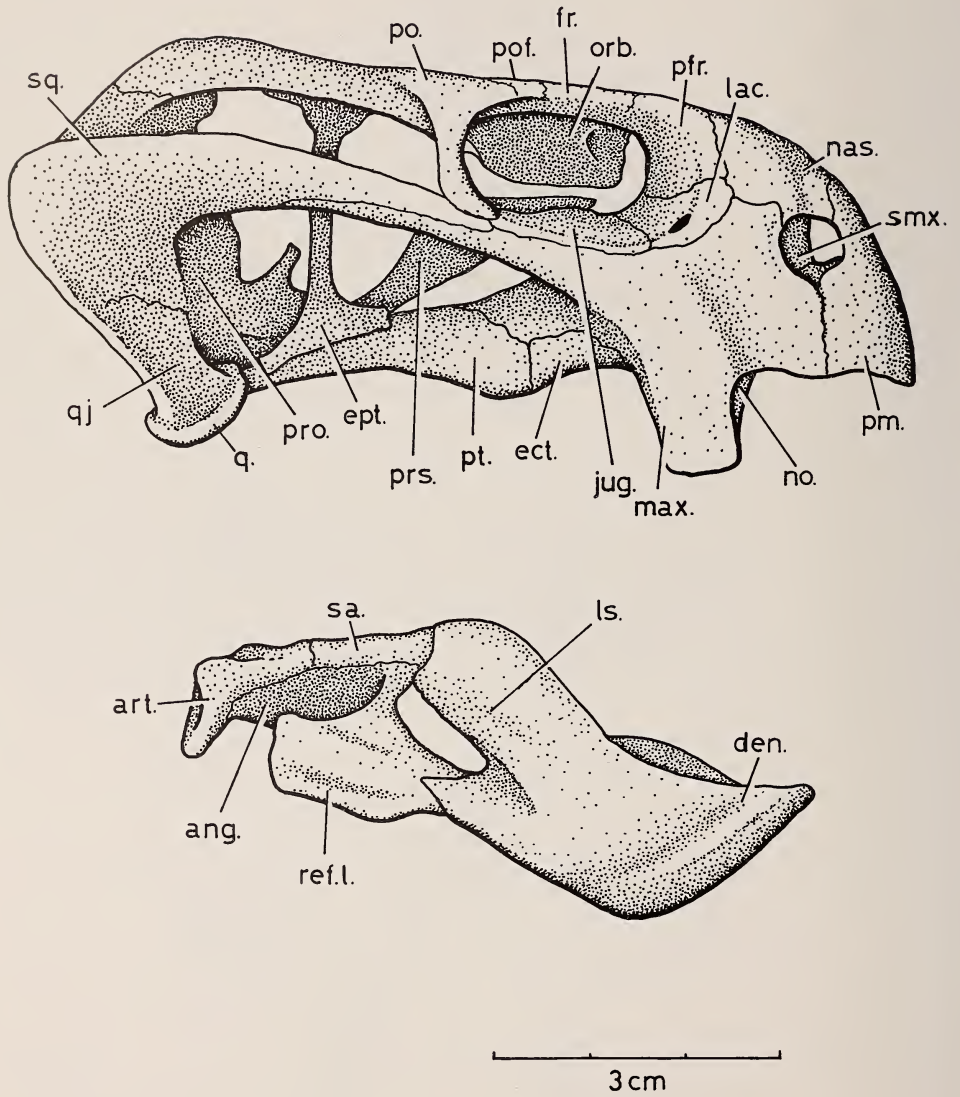


Fig. 30. *Diictodon* sp. SAM-10086. Skull and lower jaw in lateral view.

examined by M.A.C. in 1973 the anterior part of the snout was in a delicate state of preservation and it was thought unwise to loosen the several pieces of bone and matrix to verify Broom's observation.

On the skull roof the parietals are widely exposed between the postorbitals and a short wedge-shaped postfrontal is present. The palate is totally obscured and would require extensive preparation for detail to be revealed.

The lower jaw is preserved *in situ*, but few details can be made out. The symphysial region appears relatively weak.

Although this specimen is that on which Broom based the genus *Emydops*, regrettably few characters of taxonomic importance are visible. However, the name *Emydops* is now well entrenched in the literature and has become accepted as indicative of a taxon with characters that are seen in type specimens of other species currently assigned to *Emydops*. As in the case of *Pristerodon*, it is suggested here that in the interests of nomenclatural stability the name *Emydops* should be retained and the characters seen in secondary type material be included in the overall generic diagnosis.

#### *Other Emydops species*

The description of *Emydops longiceps* by Broom (1913) was based on a skull from Lemoenfontein, Beaufort West (AMNH 5578). The specimen is a weathered skull lacking lower jaw and with the occiput incomplete. The relationships between parietals, postfrontals, and frontals are easily seen. In the palate the pterygoids and palatines are crushed and broken but it is possible to provide a reasonable reconstruction. The palatal portion of the palatine is quite large and extends forward to meet the premaxilla. The vomer, which is excavated ventrally in the form of a longitudinal trough, meets the posterior tip of the median premaxillary ridge. A single small tooth is present on the maxilla close to the alveolar border. Anterior premaxillary palatal ridges are apparently absent.

*Emydops platyceps* (Broom & Haughton 1917) is based on a skull from Dunedin, Beaufort West (SAM-2667). The skull roof is complete up to the anterior third of the orbit and the relationships between the bones are essentially the same as in the previously described specimen. In the palate each maxilla bears a tusk, and there are two small postcanine teeth posteriorly on the left-hand side. The palatal portion of the palatine is quite large but broken by a notch in its medial border. The palatine reaches forward to the level of the rear of the premaxilla. Anterior premaxillary ridges are absent but a pair of longitudinal grooves runs alongside the median palatal ridge to the level of the canine tusk. The rear of the vomerine septum is trough-shaped but the more anterior part is thin and blade-like.

The description of *Emydops longus* (Fig. 31A-B) by Broom (1921) was based on a skull and lower jaw from Biesjiespoort, Victoria West (BMNH R4956). The skull is dorsoventrally crushed and the snout damaged by an early attempt at preparation. On the skull roof the parietals are very widely exposed.

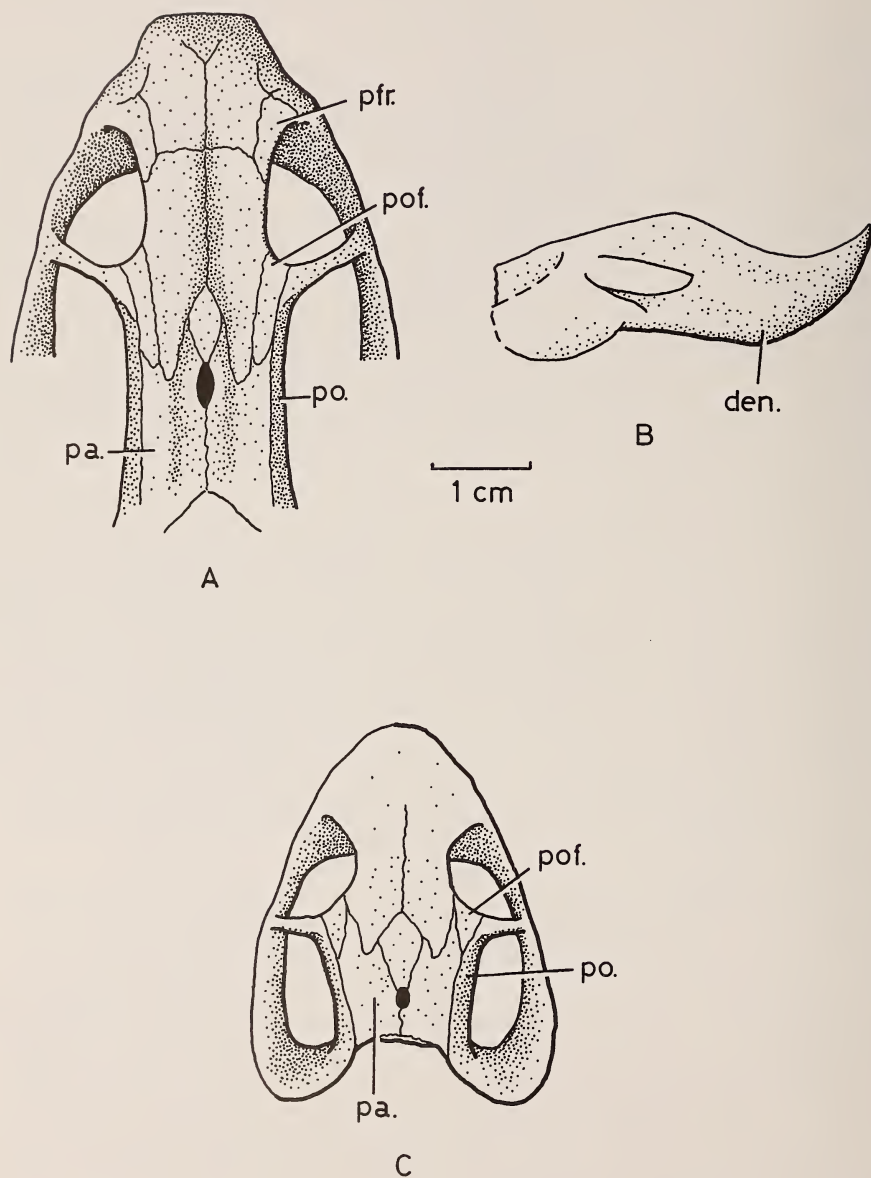


Fig. 31. A-B. *Emydops longus*. Type specimen BMNH R4956, from Biesjiespoort, Beaufort West. A. Skull in dorsal view. B. Lower jaw in lateral view. C. *Emydops minor*. Type specimen AMNH 5525, from Kuilspoort, Beaufort West. Skull in dorsal view.

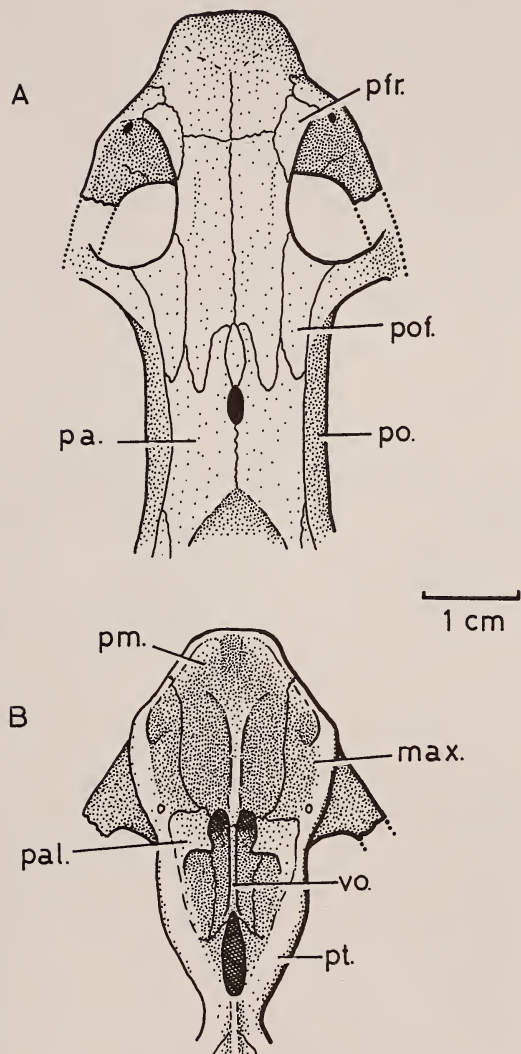


Fig. 32. *Emydops longus*. Paratype BMNH R4957, from Biesjiespoort, Victoria West. A-B. Skull in dorsal and ventral views.

The postorbitals lie along the side of the intertemporal bar, forming the medial borders of the temporal fenestra.

The palate is obscured by the lower jaw but a single tooth is visible close to the alveolar border behind the caniniform process.

The lower jaw has a prominent lateral dentary shelf and a sharp shovel-shaped symphysis. At least four teeth are present on the dorsomedial edge of the dentary. One of the teeth shows a distinct row of five posterior serrations. Because of damage during earlier preparation part of the dentary is lost and a complete tooth count is not possible.

The paratype of *Emydops longus*, (BMNH R4957, Fig. 32) adds considerable information concerning the morphology of the species. The postorbital lies on the side of the intertemporal bar, as in the type specimen, and has

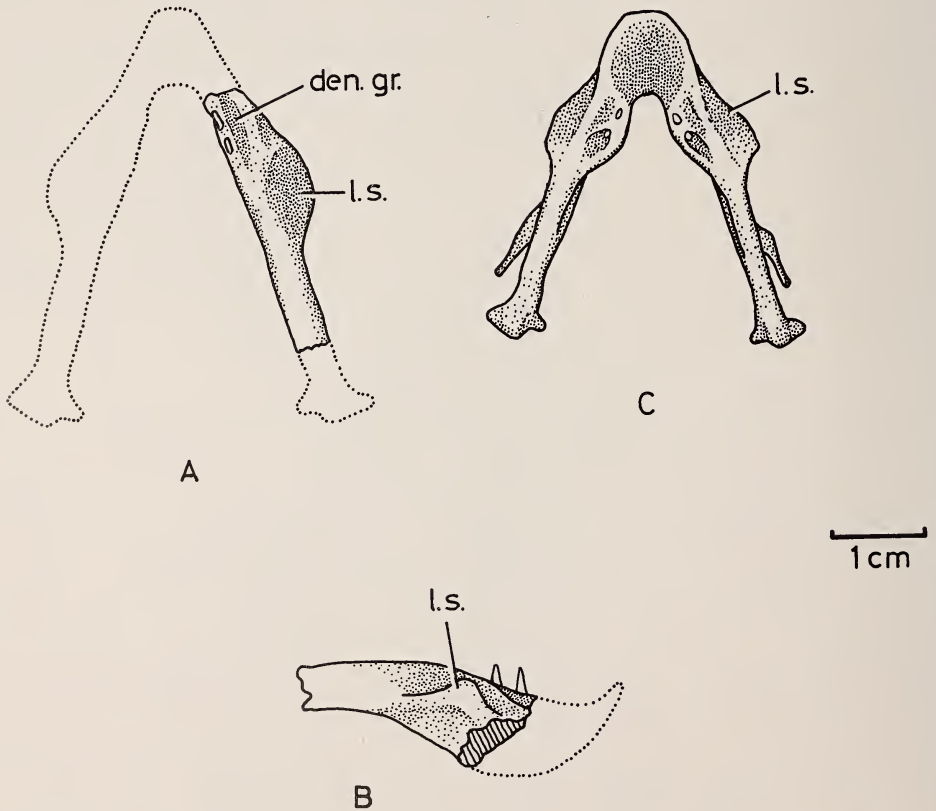


Fig. 33. A-B. *Emydops brachyops*. Type specimen SAM-708 from 'The Gough', Beaufort West. Right ramus of lower jaw in dorsal and lateral views. C. *Emydops* sp. SAM-10172, from Dunedin, Beaufort West. Lower jaw in dorsal view.



practically no dorsal skull roof exposure. The maxilla rises fairly high on the side of the snout and confines the lacrimal to the anterior border of the orbit.

In ventral view the vomer is seen to border only the anterior part of the interpterygoidal vacuity, but does not form a trough-like anterior extension of the vacuity. The palatal portion of the palatine is a horizontal plate transversely extended to form a posterior extension of the premaxillary secondary palate, making a brief contact with the premaxilla. The posterior border of the palatal portion is concave. The palatal rim is interrupted at the level of the caniniform process and a medial embayment is formed anterior to the weak caniniform

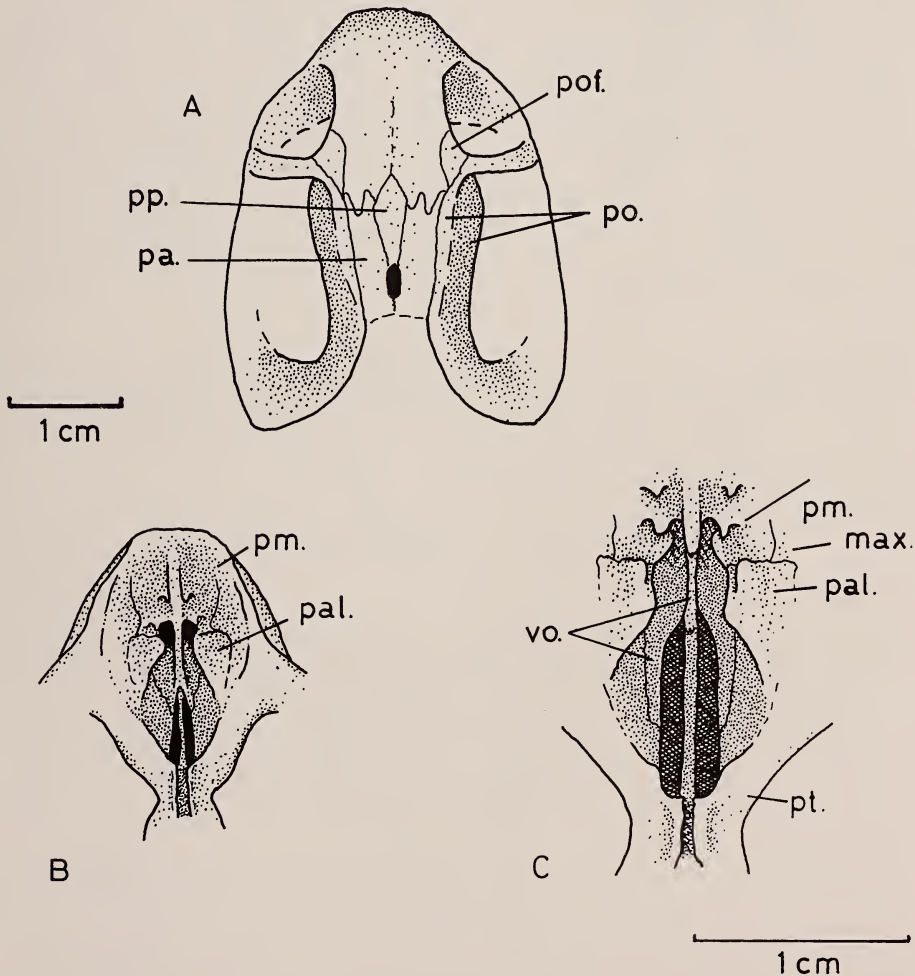


Fig. 34. *Emydops parvus*. Type specimen BMNH R4960, from Bruinjieshoogte, Somerset East. A-B. Skull in dorsal and ventral views. C. Detailed palatal view.

process. A raised ledge is formed medial to the caniniform process. A single small tooth lies behind the process, close to the alveolar border.

The lower jaws in the type specimen of *Emydops brachyops* (Broom), SAM-708 (Fig. 33A-B), and in SAM-10172 (Fig. 33C) indicate that a short, shallow groove extends back along the dorsal edge of the dentary behind the symphyseal region.

#### *Diagnosis*

Taking into account the information gained from the various species of *Emydops* described above (see also Figs 34-35), it is possible to formulate the following generic diagnosis.

Small dicynodonts with broad intertemporal region and wide parietal exposure on the skull roof. Palatine meets posterior border of premaxilla and is transversely enlarged into a horizontal plate with a concave posterior border. Anterior trough-like extension of the interpterygoidal vacuity on to the vomerine septum short or absent. Embayment in palatal rim anterior to caniniform process. Interpterygoidal crest weak, not continued on to ventral surface of anterior pterygoid ramus. Dentary shelf prominent. Anterior symphyseal region of dentary drawn up into a sharp cutting edge. Shallow groove on dorsal edge of dentary behind symphysis.

#### *Related genera*

Cluver (1974b) has discussed the possible relationships of *Emydops*, *Myosaurus*, *Myosauroides* and *Cistecephalus*. His conclusion that the last three genera are probably quite closely related and may have arisen from an *Emydops*-like ancestor, is accepted here.

### Genus *Kingoria* Cox, 1959

#### *Diagnosis*

This genus (Figs 36-38) has recently been reviewed by Cluver & Hotton (1981). Their diagnosis with minor modifications will be used here.

Medium-sized dicynodonts (average skull length 160 mm), jaws lacking teeth altogether or bearing a single pair of maxillary tusks. Parietals exposed between postorbitals behind pineal foramen. Septomaxilla recessed within opening of naris, maxilla rises high on the side of the snout to meet nasal. Low boss formed by nasal. Maxilla carries prominent caniniform process. Rear of caniniform process extended as a keel to level of ectopterygoid. Palatal rim continued without interruption on to anterior blade of caniniform process. Palatal portion of palatine very small, restricted to border of choanal depression but making contact with greatly expanded premaxilla. Vomers form short septum in interpterygoidal fossa. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries taper to form rounded anterior tip of lower jaw, no dentary tables present. Dorsal edge of dentary narrow, lateral dentary shelf

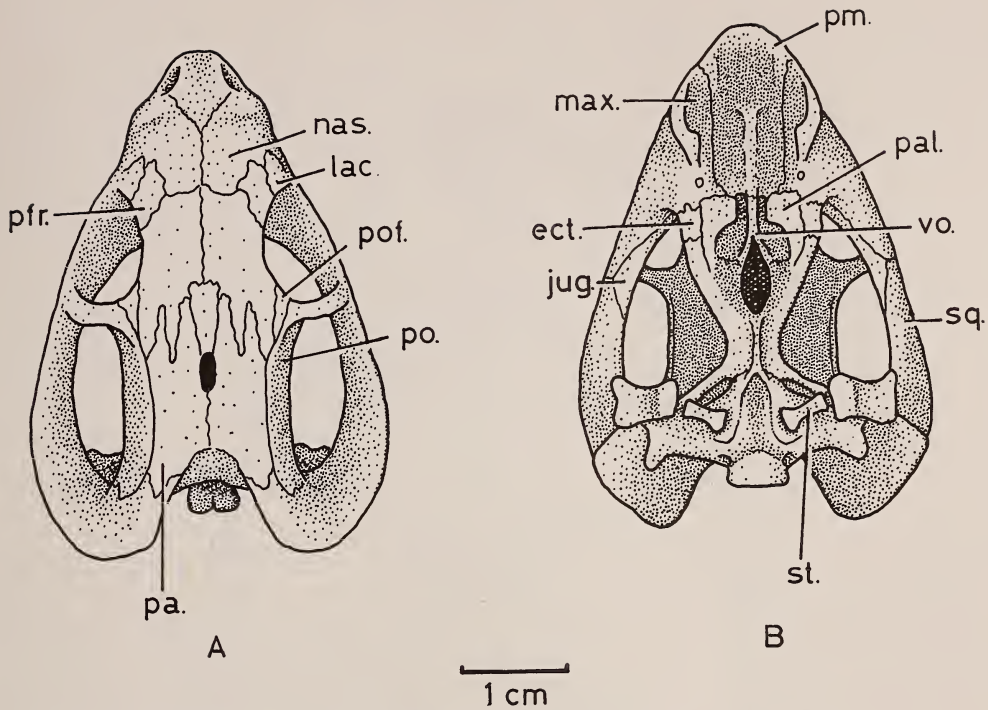


Fig. 35. *Emydops* sp. SAM-11060, from Leeuwkloof, Beaufort West. A-B. Skull in dorsal and ventral views.

widely expanded. Mandibular fenestra reduced or absent. Angular forms sharp ventral keel behind reflected lamina.

#### *Related genera*

The Lower Triassic genus *Kombuisia* (Hotton 1974) may be related to *Kingoria*. Features such as the very small contribution of the palatine to the secondary palate, the large ectopterygoid separating maxilla and pterygoid, the prominent lateral dentary shelf, and absence of the postfrontal may ally the two genera. *Kombuisia* has several specialized characters of its own, and Hotton (1974) discussed possible relationships between these two genera.

### PHYLOGENETIC ANALYSIS OF RELATIONSHIPS BETWEEN PERMIAN DICYNODONT GENERA

#### *Introduction*

Having established generic diagnoses of several Permian dicynodont genera, an attempt to draw up a scheme of the relationships between these genera may be made. Not all the characters used in the generic diagnoses prove to be

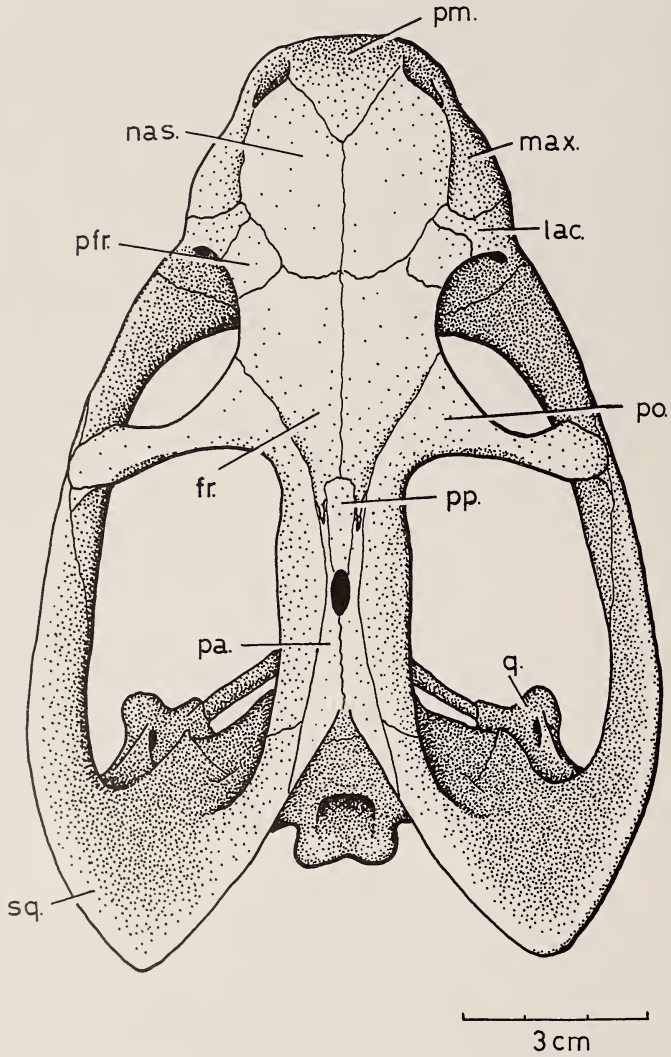


Fig. 36. *Kingoria nowacki*. Skull in dorsal view. (After Cox 1959.)

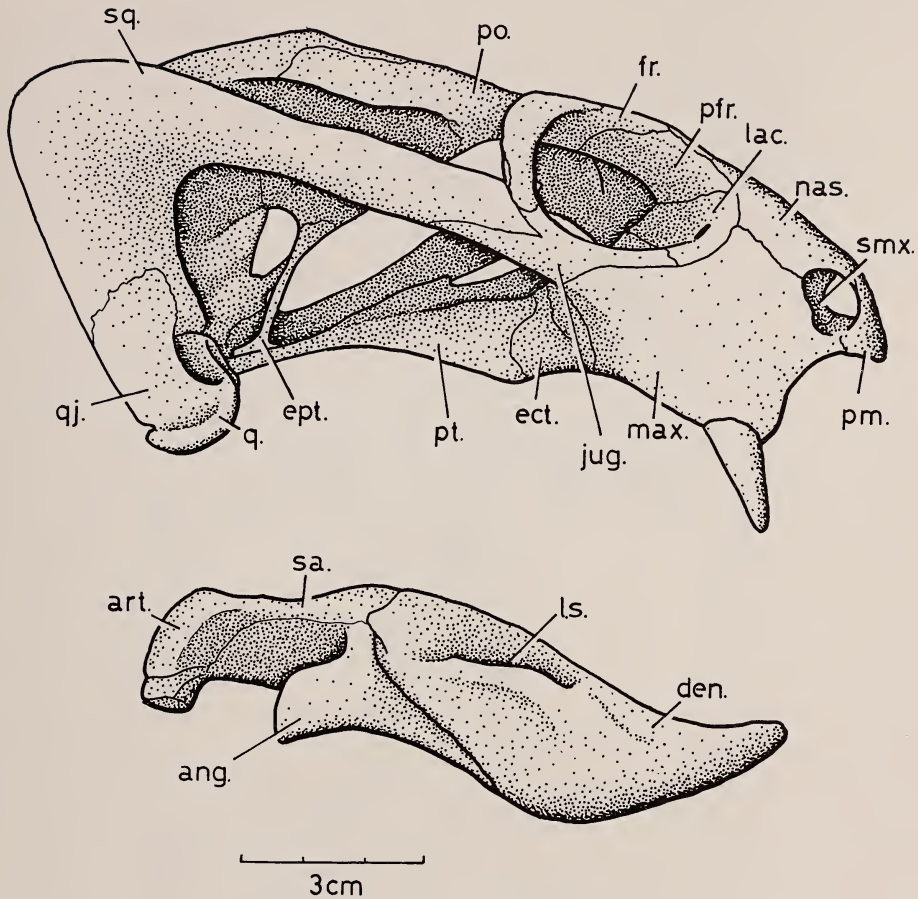


Fig. 37. *Kingoria nowacki*. Skull and lower jaw in lateral view. (After Cox 1959.)

useful in constructing a phylogeny. The characters that are useful are shown below in the character suites. Shared derived characters, where these can be determined, have been used to link related groups. The primitive condition for dicynodonts is taken to be represented most closely by *Venjukovia* (Efremov 1940).

*Venjukovia* is from Zone II of the Upper Permian of Russia and has been implicated in the evolution of dicynodonts by several workers (Watson 1948; Olson 1962; Tchudinov 1965; Barghusen 1976).

*Venjukovia* (Fig. 39) exhibits several features that are primitive for therapsids: the premaxillae are paired, the anterior dentition is present, the interptery-

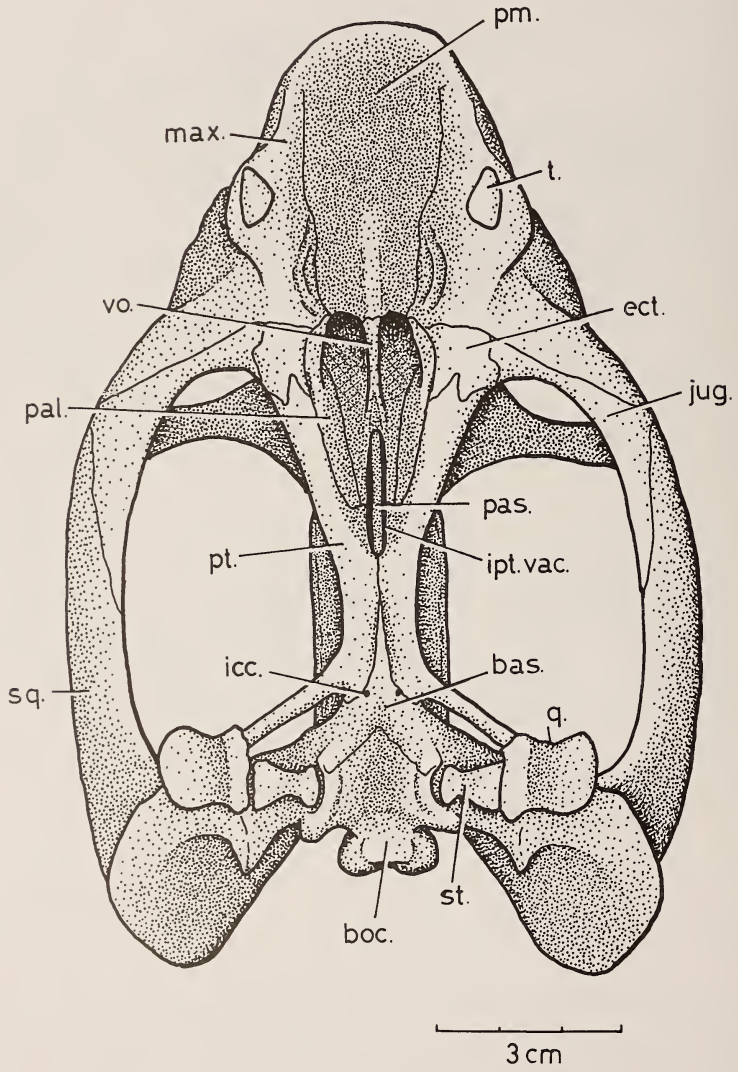


Fig. 38. *Kingoria nowacki*. Skull in ventral view. (After Cox 1959.)

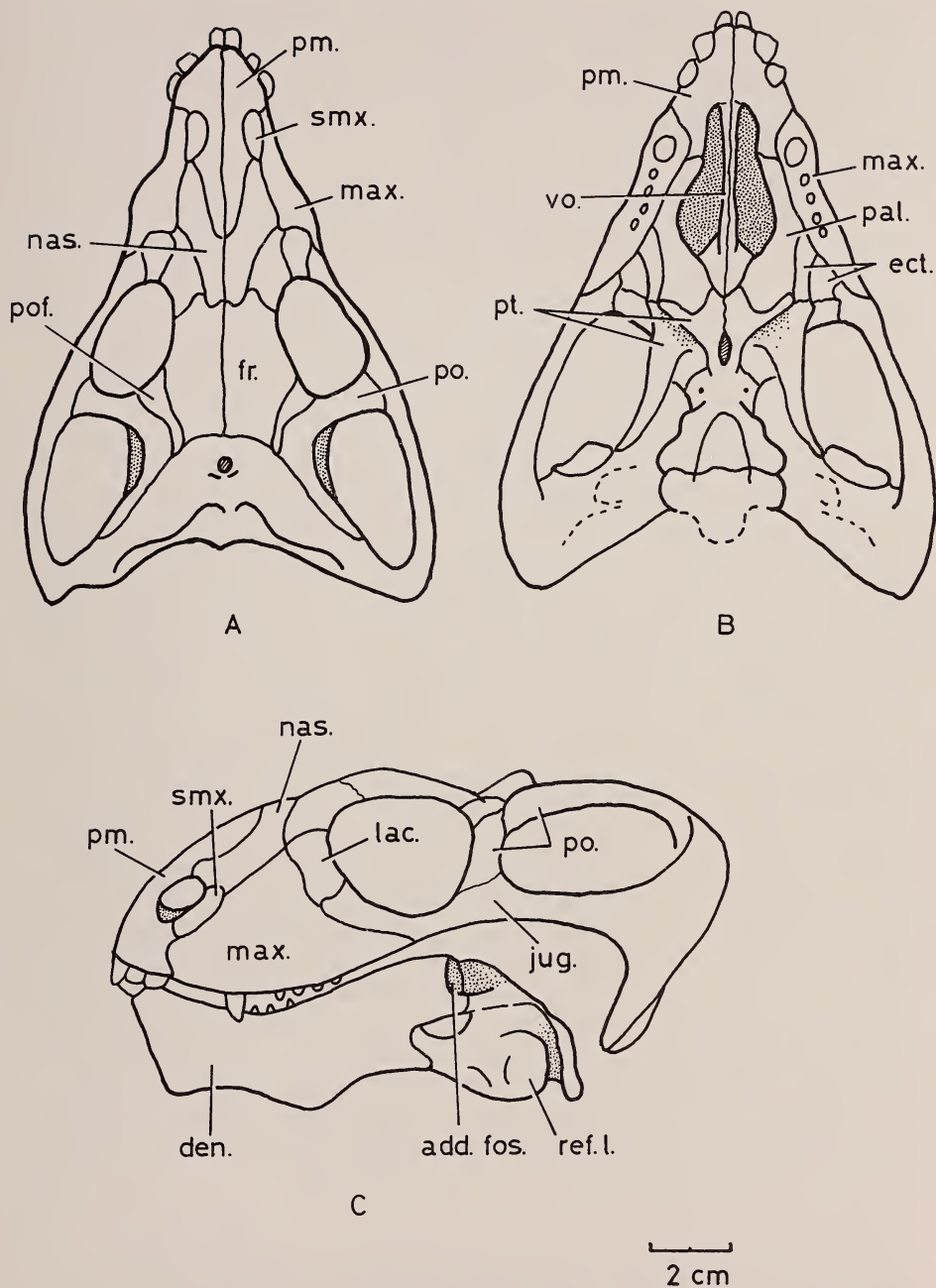


Fig. 39. *Venjukovia* sp. A-B. Skull in dorsal and ventral views. C. Skull and lower jaw in lateral view. (After Barghusen 1976.)

goidal vacuity lies wholly between the pterygoids, the adductor musculature does not extend far forward on the lower jaw, the secondary palate is not extensive compared with later dicynodonts, the lateral pterygoid process (transverse flange) is pronounced, the ventral edge of the median vomer plate bears a shallow trough, and there is no preparietal.

However, *Venjukovia* also exhibits derived characters that ally it with later dicynodonts: the coronoid bone is absent, the preorbital region is short, the lateral pterygoid process is modified and directed anteriorly, the zygoma is emarginated ventrally, musculature attaches to the external surface of the zygoma and to the external surface of the dentary posteriorly, the lower jaw articulation is modified, possibly permitting a sliding action, there is an incipient secondary palate with the palatine beginning to assume a role forming a partial floor to the internal nares as it extends forward and slightly medially, a mandibular fenestra is present, and palatal teeth are lost.

Some of these features may be adaptations for herbivorous feeding, for example the short preorbital region, the reduction and modification of the lateral pterygoid flange, and the low blunt teeth, and there is therefore the possibility that they have evolved in parallel in *Venjukovia* and dicynodonts. However, it is felt that in view of the number of derived characters linking them, it is more parsimonious to assume that the two groups are related. As stated at page 197, the derived character suite given above is taken to define the Dicynodontia, and *Venjukovia* is therefore considered to be a dicynodont.

*Venjukovia* is here taken to represent an initial stage in the evolution of the later dicynodont groups, and is used for comparison with these later forms that express more fully the dicynodont characters outlined in the Introduction (p. 196).

Little more can be said about *Venjukovia* until a full description is published, since the present authors do not have access to the type specimens.

*Otsheria netzvetajevi* is another Russian taxon that has been implicated in dicynodont evolution. It is from the Ocher deposits (early Upper Permian) and was described by Tchudinov (1960). It resembles *Venjukovia* in certain respects, such as preorbital shortening and the emarginated zygoma, and these features indicate dicynodont affinity. The lateral pterygoid process is stronger in *Otsheria* and the palatine is not incorporated into the secondary palate, but the premaxilla extends further back to produce an incipient secondary palate.

As with *Venjukovia*, primary type material could not be examined and, although *Otsheria* is here considered to be related to the rest of the Dicynodontia, precise relationships cannot be determined at present.

#### *Character suites*

The following character suites were drawn up for each of the major genera described earlier. Each suite is designated with a letter and these letters appear on the suggested cladogram along the relevant line as depicted in Figure 40. All characters noted are thought to represent characters derived with respect to



*Venjukovia*, except suite A, which represents the characters of *Venjukovia* that are derived with respect to primitive therapsids.

At certain points tentative functional explanations for the changes in morphology are given.

*Suite A*

- (i) Preorbital shortening,
- (ii) the lateral pterygoid process reduced and anteriorly directed,
- (iii) emargination of the zygoma,
- (iv) loss of the coronoid bone,
- (v) jaw articulation that permits a sliding action,
- (vi) presence of a mandibular fenestra.

These features are probably related to the adoption of a herbivorous diet and to the need to increase the moment arm of the jaw adductor musculature. In contrast to other therapsids, dicynodonts have increased the moment arm not by the acquisition of a coronoid process (DeMar & Barghusen 1973) but by forward migration of the adductor insertion. This innovation is probably the key to understanding the specialized morphology of the dicynodont skull. Migration of the adductor insertion has consequences on skull structure, such as shortening of the tooth row and encroachment of the jaw musculature on the preorbital region, which are avoided if a coronoid process develops. These consequences seem to have been accepted in the dicynodont skull and capitalized upon to produce a masticatory mechanism that is suited to herbivorous feeding (King 1981).

The lateral pterygoid process might have been reduced as a consequence of, or as a prerequisite to, modification of the area of origin of the posterior pterygoideus muscle. In early therapsids such as *Titanophoneus*, the pterygoideus musculature attached to the quadrate rami of the pterygoids, and also to the posterior surfaces of the lateral pterygoid processes (Barghusen 1976). Barghusen argues that the anterior pterygoid processes of dicynodonts are modified (i.e. anteriorly directed) lateral pterygoid processes and assumes that the origin of the pterygoideus musculature is carried forward as the lateral pterygoid process is modified. A more anterior origin will enhance the forward-pulling component of this muscle, provided that the insertion remains approximately in the same position. The forward component of the pterygoideus musculature plays an important part in the masticatory cycle in protracting the jaw (King 1981) and in stabilizing the jaw articulation (Crompton & Hotton 1967).

*Suite B*

- (i) Loss of teeth on anterior part of maxilla,
- (ii) medial migration of postcanine teeth,
- (iii) shallow longitudinal depression on dorsal surface of dentary,
- (iv) vomers form anterior part of interpterygoidal vacuity,

- (v) palatines enlarged and form part of secondary palate,
- (vi) articular-quadrate joint elaborated to permit extensive sliding action
- (vii) medial articular condyle enlarged,
- (viii) reduction of preorbital region carried further,
- (ix) temporal fenestra elongated,
- (x) zygoma further emarginated,
- (xi) development of a plate-like lateral extension of squamosal,
- (xii) dentary with built-up area on its lateral surface for insertion of the adductor musculature.

Features (i) to (iii) are associated with the acquisition of the dicynodont horny beak, and features (iv) and (v) with the beginning of the secondary palate. Features (vi) and (vii) probably reflect the elaboration of the dicynodont masticatory pattern so that an extensive sliding action is permitted, but at the same time the medial articular condyle is enlarged to help prevent dislocation of the jaw-hinge (King 1981). Features (viii) to (xii) reflect the acquisition of the typical dicynodont pattern of jaw musculature with a branch of the adductor externus originating from the external surface of the zygoma, and a branch originating more medially from the temporal region of the skull. The insertion of the lateral branch would have been on the built-up lateral surface of the dentary (Cluver 1975; Crompton & Hotton 1967; King 1981).

All the features may be seen in the context of improving the masticatory system as an adaptation to the efficient mastication of plant material.

*Suite C (defining Eodicynodon)*

- (i) Further loss of premaxillary teeth,
- (ii) palatal exposure of the palatine bulbous and rugose,
- (iii) mid-ventral palatal plate of the vomers swollen posterior to its junction with medial premaxillary process,
- (iv) pterygoids extended ventrally into a powerful rugose boss anterior to internal carotid artery foramina,
- (v) built-up area on dentary elaborated into a dorsal ledge projecting above general surface of jaw ramus,
- (vi) cleft in maxillary rim anterior to canine tusk.

*Suite D*

- (i) Premaxillae fused,
- (ii) lateral pterygoid process reduced,
- (iii) insertion of lateral external adductor migrates forward,
- (iv) stapedia foramen lost.

This stage represents further elaboration of the horny beak as more teeth are lost. There is also further increase in the bite force as the insertion of the adductor externus lateralis migrates anteriorly.

Reduction of the lateral pterygoid process may reflect a further modification in the area of origin of the pterygoideus muscles, or it may indicate a

reduced role in the process of the bracing and control of movement of the lower jaw (Barghusen 1976). This control might have been less essential since the foodstuff ingested would have been passive and (more importantly) because muscles were taking over the role of controlling jaw movements.

*Suite E (defining Endothiodon)*

- (i) Teeth lie in a row posterior to the caniniform process, with the anterior teeth on the premaxilla,
- (ii) intertemporal region with postorbitals overlapping parietals,
- (iii) front margin of palate bears deep median notch,
- (iv) secondary palate vaulted,
- (v) groove lateral to upper tooth row,
- (vi) anterior portion of lower jaw forms a sharp beak,
- (vii) lower jaw bears long teeth in a row,
- (viii) lower jaw bears dorsal dentary trough lateral to tooth row.

*Suite F*

- (i) Premaxillary teeth lost,
- (ii) palatines extended medially and become incorporated into the rear of the secondary palate.

*Suite G*

- (i) Longitudinal groove in dorsal edge of dentary modified into a deep, thin-walled sulcus.

The real function of this groove is at present obscure but it is most probably implicated either with the attachment of the horny beak (King 1981) or with the adductor muscle insertion (Crompton & Hotton 1967; Cluver 1971). In either case it would be involved with improvement of the feeding mechanism.

*Suite H (defining Pristerodon)*

- (i) Built-up area on dentary enlarged into prominent dentary shelf,
- (ii) palatine large and leaf-like and receives bite of lower teeth,
- (iii) palatal teeth arranged in short row at an angle to longitudinal axis of palate.

*Suite I*

- (i) Dentary built up dorsally into tables in front of dentary sulcus,
- (ii) maxillary rim extended ventrally, forming a close fit with lower jaw symphysis when closed,
- (iii) anterior premaxillary ridges present.

These changes probably represent adaptations to a feeding pattern with precise cutting and crushing actions between upper and lower beaks.

The palatal area (including the palatines) is also used for mastication.

*Suite J*

- (i) Postcaniniform crest present,
- (ii) nasal bosses present.

The extension of the palatal rim posteriorly as a sharp-edged crest could be involved with mastication either by increasing the length of the cutting edge between upper and lower beaks or by providing attachment for a muscular cheek that would help to retain partly chewed plant matter during mastication (Cluver 1975).

*Suite K (defining Tropidostoma)*

- (i) Postorbitals overlap parietals, producing a narrow intertemporal region, where the parietal exposure lies within a groove.

Many specimens of *Tropidostoma* are tuskless but retain the other features of the genus. It is not clear whether this constitutes a sexual dimorphism or not.

*Suite L*

- (i) Postcanine teeth lost,
- (ii) tusks lost,
- (iii) vomerine trough closes and vomerine septum becomes narrow.

The second feature may be related either to loss of a secondary sexual feature or with modification of the feeding mechanism perhaps associated with the complete loss of the postcanine teeth.

*Suite M (defining Rhachiocephalus)*

- (i) Increase in size,
- (ii) presence of a pineal boss,
- (iii) narrow intertemporal region with postorbitals tending to meet behind the pineal boss.

*Suite N (defining Oudenodon)*

- (i) Anterior extension of the interpterygoidal vacuity short, vomerine septum short.

*Suite O*

- (i) Labial fossa present,
- (ii) postcanine teeth lost,
- (iii) vomerine septum narrow,
- (iv) intertuberal ridge present.

*Suite P (defining Aulacephalodon)*

- (i) Parietal with wide exposure on skull roof,
- (ii) postorbital narrow and closely applied to the steep-sided intertemporal bar,

- (iii) elaborate nasal bosses present,
- (iv) skull broad,
- (v) zygoma bears boss,
- (vi) spur of jugal ascends into postorbital bar.

*Pelanomodon* is very similar to *Aulacephalodon* except that it is tuskless and has lost the anterior palatal premaxillary ridges. The exact relationship to *Aulacephalodon* has not yet been determined.

*Suite Q (defining Dicynodon)*

- (i) Narrow intertemporal region,
- (ii) palatal exposure of palatine flat,
- (iii) lower jaw bears lateral dentary ledge.

Triassic representatives of the *Dicynodon* line.

Genera such as *Lystrosaurus*, *Kannemeyeria*, etc., possess features of the *Dicynodon* line and have their own derived features:

- (i) Basicranial axis shortened,
- (ii) snout deepened,
- (iii) snout lengthened,
- (iv) overall size increased.

*Suite R*

- (i) Size of palatal exposure of palatine reduced,
- (ii) marginal postcanine teeth lost.

The palatine area was probably not used so extensively for mastication, which instead took place on the maxilla medial to the tusk or caniniform process.

*Suite S*

- (i) Maxilla bears an embayment anterior to caniniform process or tusk.

The embayment might have arisen as a result of the maxilla being enlarged medially to form new crushing areas for the lower jaw, or it might have served for better attachment of the horny beak.

*Suite T*

- (i) Built-up area on dentary dorsally placed and forms dentary shelf,
- (ii) anterior edge of symphysis drawn up into sharp cutting edge,
- (iii) vomerine septum short and narrow,
- (iv) palate bears grooves either side of median pre-maxillary ridge.

*Suite U*

- (i) Teeth of upper jaw reduced,
- (ii) anterior rami of pterygoids straight and elongate,
- (iii) basicranial region shortened.

*Suite V (defining Myosaurus)*

- (i) Absence of teeth in upper and lower jaws,
- (ii) medial extent of palatine small so that palatine is confined to lateral border of choanal depression,
- (iii) anterior border of orbit extends inward to close off back of snout.

*Suite W (defining Emydops)*

- (i) Palatal exposure of palatine a flat, horizontal plate with concave posterior border.

*Suite X (defining Cistecephalus)*

- (i) Palatines reduced posteriorly and premaxilla extends back beyond root of zygoma,
- (ii) stapedia foramen present,
- (iii) fossae present at the base of zygoma,
- (iv) interpterygoid vacuity reduced or lost,
- (v) skull roof wide,
- (vi) teeth absent.

*Suite Y*

- (i) Maxillary embayment extended into a notch,
- (ii) dorsal longitudinal dentary groove lost,
- (iii) maxillary rim extended ventrally to form caniniform process.

*Suite Z (defining Diictodon)*

- (i) Absence of postcanine teeth,
- (ii) anterior part of palatal exposure of palatines greatly reduced,
- (iii) dentary table prominent with medial edge built up higher than lateral edge,
- (iv) built-up area on lateral surface of dentary weak and low down on jaw,
- (v) anterior palatal ridges present,
- (vi) postorbitals overlap parietals producing a narrow intertemporal region,
- (vii) caniniform process blade-like,
- (viii) ventral keel on anterior pterygoid ramus.

*Suite A<sup>1</sup> (defining Robertia)*

- (i) Built-up area on lateral surface of dentary ledge-like and occludes mandibular fenestra.

*Suite B<sup>1</sup> (defining Kingoria)*

- (i) Absence of postcanine teeth,
- (ii) dentary shelf large,
- (iii) dorsal edge of lower jaw sharp,
- (iv) palatal exposure of palatine reduced so that it is confined to lateral border of choana,
- (v) mandibular fenestra closed up,
- (vi) lower beak sharp and shovel-shaped,
- (vii) thin plate-like ventral extension to anterior pterygoid ramus,
- (viii) maxilla bears ventral keel posterior to caniniform process.

A cladogram (Fig. 40) has been drawn up, using the character suites set out above.



Fig. 40. Cladistic interpretation of the relationships between Permian Dicynodontia.

A CLASSIFICATION OF DICYNODONTS

In erecting the following classification from the cladogram, each successive group diverging from the main axis (A-B<sup>1</sup>) has been given equal rank as a suborder. Along each main divergent line secondary divergent lines have been given the rank of superfamily, tertiary lines that of family, and quaternary lines that of subfamily.

This sequential method of classification has been used, first, because the detailed taxonomic picture of dicynodonts is far from complete and, secondly, because any classification should be able to accommodate newly discovered specimens. It should be possible to add other taxa to this classification at a future date without disturbing its hierarchical order. This procedure also obviates the necessity of proposing several completely new taxon names.

Some notes are necessary concerning the use of the term Dicynodontia instead of Anomodontia, the raising of the Dicynodontia to subordinal status, and the inclusion of the Venjukoviamorpha within the Dicynodontia.

Owen (1859) erected the order Anomodontia for animals without teeth (except possibly tusks or caniniform processes) with a parietal foramen, two nostrils, and a fixed tympanic pedicle. He included three families within the order: the Dicynodontia (*Dicynodon* and *Ptychognathus* = *Lystrosaurus*), the Cryptodontia (*Oudenodon*), and the Gnathodontia (*Rhynchocephalus*).

In 1861 Owen modified this classification, excluding the Gnathodontia and including the Cynodontia for forms such as *Galesaurus*. Owen in 1876 again modified this classification, renaming the Dicynodontia the Bidentalia and including only this family, the Dicynodontia, and a new family the Endothiodontia (for *Endothiodon*).

Seeley (1889, 1894), Lydekker (1890), and Nicholson & Lydekker (1899) included further families within the Anomodontia, but Broom (1905) stressed that many of these families did not fall within the original definition that Owen used for the Anomodontia, and suggested that only forms allied to *Dicynodon* (i.e. *Oudenodon*, *Lystrosaurus*, etc.) should be included.

Broom's (1905) classification of Therapsida stood with little change until the classification of Watson & Romer (1956). These authors divided the Therapsida into the Theriodontia and the Anomodontia, which included the 'dicynodonts' (equivalent to Broom's (1905) Anomodontia), the dromasaurs, and the herbivorous dinocephalians. A new infraorder, the Dicynodontia, was erected within the suborder Anomodontia. The present authors feel that the evidence for dividing the herbivorous from the carnivorous dinocephalians, and for associating the herbivorous forms with the dicynodonts is very inconclusive, and propose that all dinocephalians be retained within the taxon Dinocephalia and that this taxon and the Dicynodontia be considered as independent suborders of the order Therapsida. It is further suggested that since the term Dicynodontia is now in common usage it be used in preference to Anomodontia, which would become a *nomen nudum*.

*Venjukovia* has been included (with *Otsheria*) in the infraorder Venjukoviamorpha (Romer 1966). This infraorder has equal ranking with the Dicynodontia in Romer's classification. It was argued earlier in the present work that *Venjukovia* exhibits features that link it closely with dicynodonts and that it should be included within the Dicynodontia. Accordingly, the infraorder Venjukoviamorpha is here included in the suborder Dicynodontia.



## Order THERAPSIDA

## Suborder DICYNODONTIA nov.

- Infraorder VENJUKOVIAMORPHA Romer, 1966  
*Venjukovia* Efremov, 1940  
*Otsheria* Tchudinov, 1960
- Infraorder EODICYNODONTIA nov.  
*Eodicynodon* Barry, 1974
- Infraorder ENDOTHIODONTIA nov.  
*Endothiodon* Owen, 1876  
*Pachytegos* Haughton, 1932  
*Chelydontops* Cluver, 1975

## Infraorder PRISTERODONTIA nov.

## Superfamily DICYNODONTOIDEA nov.

Family **Cryptodontidae** Owen, 1859

## Subfamily Tropidostominae nov.

*Tropidostoma* Seeley, 1889

## Subfamily Pelorocyclopinæ

*Rhachiocephalus* Owen, 1876

van Hoepen, 1934

## Subfamily Oudenodontinae nov.

*Oudenodon* Owen, 1869Family **Aulacephalodontidae** nov.

## Subfamily Aulacephalodontinae

*Aulacephalodon* Owen, 1844

Toerien, 1953

## Subfamily Pelanomodontinae nov.

*Pelanomodon* Broom, 1938Family **Dicynodontidae** Owen, 1859*Dicynodon* Owen, 1845Family **Kannemeyeriidae** von Huene, 1948

Triassic forms

Family **Pristerodontidae** nov.*Pristerodon* Huxley, 1868*Emyduranus* Broom, 1921*Synostocephalus* Broili &

Schröder, 1935

## Infraorder DIICTODONTIA nov.

## Superfamily EMYDOPOIDEA nov.

Family **Emydopidae** nov.

## Subfamily Emydopinae nov.

*Emydops* Broom, 1912

## Subfamily Myosaurinae nov.

*Myosaurus* Haughton, 1917*Myosauroides* Broom, 1941Family **Cistecephalidae** Toerien, 1953*Cistecephalus* Owen, 1876*Cistecephaloides* Cluver, 1974a*Kawingasaurus* Cox, 1972

## Superfamily ROBERTOIDEA nov.

Family **Robertiidae** nov.*Robertia* Boonstra, 1948Family **Diictodontidae** nov.*Diictodon* Broom, 1913

## Infraorder KINGORIAMORPHA nov.

*Kingoria* Cox, 1959*Kombuisia* Hotton, 1974

*Incertae sedis*

- Gordonia* Newton, 1893 (possibly related to *Kingoria* or *Dicynodon*)  
*Eosimops newtoni* Broom, 1921  
*Cryptocynodon simus* Seeley, 1894  
*Koupia* Boonstra, 1948  
*Brachyuraniscus* Broili & Schröder, 1935  
*Broilius* Toerien, 1953  
*Ceraetulus mirabilis* Broom, 1931  
*Palemydops* Broom, 1921 (related to *Emydops*)  
*Aulacocephalus pithecopus* Seeley, 1898  
*Compsodon helmoedi* van Hoepen, 1934  
*Eurychororhinus boonstrai* Broili & Schröder, 1935 (possibly *Pristerodon*)  
*Prodicynodon* Broom, 1904 (possibly related to *Endothiodon* or *Chelydon-*  
*tops*)  
*Taognathus megalodon* Broom, 1911  
*Eumantellia mirus* Broom, 1911  
*Newtonella platyceps* Broom, 1937  
*Heuneus oudebergenis* Toerien, 1953

Premaxillary teeth have been recorded in *Eumantellia*, *Newtonella* and *Heuneus*. If correct, this will warrant a new infraorder. However, it is more likely that these are maxillary teeth that happened to erupt through the premaxilla. Little more can be said about the status of these forms until more material has been prepared.

- Parringtoniella broomi* Toerien, 1953  
*Emydorhinus fragilis* Broom, 1935 (type specimen cannot be traced)  
*Emydorhinus sciuroides* Broom, 1921, 1935  
*Dicynodontoides* Broom, 1940 (probably *Kingoria*, see Cluver & Hotton  
 1981)  
*Digaladon* Broom & Robinson, 1948 (possibly a juvenile *Aulacephalodon*)  
*Haughtoniana magna* Boonstra, 1938 (type specimen is indeterminate)  
*Anomodon* Keyser, 1975 (erected on the basis of the description of  
*Dicynodon heunei* Broili & Schröder, 1937; may be related to *Rob-*  
*ertia* or *Diictodon*)  
*Storthygognathus* Janensch, 1952 (probably related to *Pristerodon*).

## CONCLUSIONS

The classification erected in the present work is considered to be definitive in that it is hoped that its major divisions will not change. However, new taxa must be incorporated as they become known or better understood and this will inevitably lead to slight modifications in the classification. The need for specific revision within the Dicynodontia remains very evident. This has not been attempted in the present work and, in addition, certain genera have been left *incertae sedis* because they are either badly preserved or inadequately prepared.

It is hoped that future modifications of the classification will be based on well-prepared primary type material.

With the establishment of a definitive classification, the groups involved can be used in a more meaningful way in ecological, palaeogeographical, and functional anatomical contexts.

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## ABBREVIATIONS

add. fos.	adductor fossa	jug.	jugal
ang.	angular	lab. fos.	labial fossa
art.	articular	lac.	lacrimal
b.	boss	lat. pal. f.	lateral palatal fenestra
bas.	basisphenoid	l.s.	lateral shelf
boc.	basioccipital	max.	maxilla
den.	dentary	max. gr.	maxillary groove
den. gr.	dentary groove	no.	notch
den. s.	dentary sulcus	op.	opisthotic
den. t.	dentary table	orb.	orbitosphenoid
ect.	ectopterygoid	pa.	parietal
eoc.	exoccipital	pal.	palatine
ept.	epipterygoid	pas.	parasphenoid
for. mag.	foramen magnum	poc.	postcaniniform crest
fr.	frontal	pfr.	prefrontal
ioc.	canal for internal carotid artery	pm.	premaxilla
ip.	interparietal	po.	postorbital
ipt. vac.	interpterygoid vacuity	pof.	postfrontal
itr.	intertuberal ridge	pp.	preparietal
		pro.	prootic

pres.	presphenoid	to.	tooth
pt.	pterygoid	tab.	tabular
pt. f.	posttemporal fenestra	vo.	vomer
q.	quadrate	VII f.	foramen for facial nerve
q.j.	quadratojugal	AMNH	American Museum of Natural History
ref. l.	reflected lamina	BMNH	British Museum (Natural History)
sa.	surangular	ROZ	Roy Oosthuizen Collection, South African Museum
smx.	septomaxilla	SAM	South African Museum
soc.	supraoccipital		
sq.	squamosal		
st.	stapes		
t.	tusk		